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FINAL REPORT

W-100-R

PRODUCTIVITY OF MISSISSIPPI VALLEY POPULATION CANADA GEESE

Prepared by:

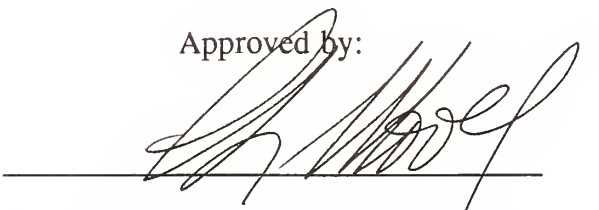
John G. Bruggink and Thomas C. Tacha

Presented to:

Illinois Department of Conservation

September, 1991

Approved by:



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STATE OF ILLINOIS

W-100-R

Project Period: July 1, 1989 through June 30, 1991

Study Title: Productivity of Mississippi Valley Population Canada Geese

Prepared by John G. Bruggink and Thomas C. Tacha
Cooperative Wildlife Research Laboratory
Southern Illinois University at Carbondale

Need:

Three aerial surveys have been conducted annually in Ontario to acquire information on reproductive activities of MVP geese. These include May surveys for numbers of prebreeding geese along the Hudson and James Bay coasts, April-May snow cover surveys along coastal inland transects, and July surveys to photograph brood flocks. The July photos provide juvenile/adult ratios in brood flocks that constitute the only productivity data used by the Mississippi Flyway Council to predict fall flights of MVP geese (Lumsden, H. G., MVP goose production surveys, 1980-1986, Unpubl. Reps.). Comparisons to July age ratios from previous years are used to discriminate "below average, average, or above average" goose production. This assessment of productivity is then combined with the previous "midwinter inventory" to predict fall flights of MVP geese.

Unbiased quantitative prediction of the fall flight of MVP geese will require reliable estimates of numbers of young produced annually. The goal of this project is to better understand productivity of MVP geese through studies of nesting and brood rearing biology, with the specific purpose of providing quantitative annual productivity estimates.

Objectives:

1. To describe nesting density, success, and phenology, and hatching success; effects of environmental factors on these productivity variables; and habitat selection of MVP Canada geese during nesting.

2. To estimate brood survival and describe habitat selection during brood rearing in 1989 and 1990.

3. To produce quantitative productivity estimates for MVP geese in 1989 and 1990.

EXECUTIVE SUMMARY

The Cooperative Wildlife Research Laboratory at SIUC, Moosonee District of the Ontario Ministry of Natural Resources, and the Illinois Department of Conservation began cooperative research spring 1985 on MVP nesting ecology at a study area near Winisk on the Hudson Bay coast of Ontario. The initial studies provided background information that led to this research project.

The project consisted of 4 studies: Study I - Nesting Ecology of MVP Canada Geese; Study II - Brood-rearing Ecology of MVP Canada Geese; Study III - Analysis of Aerial Surveys; and Study IV - Analysis and Reporting. By prior agreement, the objectives of the latter study are being met through the format of this final report. Studies I and II are reported in the form of a Disssertation submitted by John G. Bruggink in partial fulfillment of the requirements for a PhD in Zoology at SIUC. Study III is reported in the form of an accepted manuscript by Tacha et al. (1991) that was presented at, and will be published as Proceedings of the International Canada Goose Symposium. Both the dissertation and the manuscript are appended.

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INTRODUCTION

The Mississippi Valley Population (MVP) of Canada geese (Branta canadensis interior) is one of the most numerous and economically important populations of Canada geese in North America (Raveling and Lumsden 1977, Tacha 1991). Appropriate management of MVP geese requires understanding their population dynamics. Numerous studies have been conducted on MVP geese, but there is relatively little productivity information available.

Raveling and Lumsden (1977) directed their study at breeding ecology of MVP geese, but subsequent banding studies and radio-telemetry indicated the primary MVP nesting range was north of their study area at Kinoje Lake, and that the geese they studied by were primarily from the Tennessee Valley Population (Bartelt et al. 1984, Tacha et al. 1988). Tacha et al. (1988) found that 84% of the MVP nested within 80 km of the coasts of Hudson and James bays. No intensive studies on the nesting ecology of these birds were conducted prior to this study.

Raveling and Lumsden (1977) studied nesting ecology of interior Canada geese, but their study took place in inland habitats (about 460 km southeast of the where this study took place), rather than the coastal habitats used by much of the MVP. Considerable differences in the timing of spring thaw exist between the Hudson Bay coast and inland areas because of the cold maritime climate influenced by an ice pack in the bay that persists throughout much of the year (Danielson 1971, Sims et al. 1987). Differences in factors that influence goose productivity (e.g., nesting chronology, nest site selection, clutch sizes, predation pressure) probably also exist between coastal and more inland habitats.

Obtaining information on breeding (nesting and brood-rearing) ecology is necessary to understand annual variation in productivity of MVP geese. Techniques and surveys are currently (1991) being developed to provide quantitative estimates of annual production and fall flights of the MVP (Tacha et al. in press), and information presented here will be an integral part of the calculation of these estimates.

The size of the MVP has nearly quadrupled in recent years. Mid-December Goose Surveys indicated the population increased from 251,000 in 1983 to about 1.1 million in 1990 (Tacha and Thornburg in press). Such dramatic increases suggest the possibility that the population may be approaching or exceeding the average annual carrying capacity of some portion of its annual range. While several studies of the feeding ecology of northern nesting geese have been conducted in recent years (e.g., Jefferies et al. 1979; Prevett et al. 1979, 1985; Thomas and Prevett 1980; Cargill and Jefferies 1984b; Sedinger and Raveling 1984, 1986; Bazely and Jefferies 1985, 1986, 1989; Hik and Jefferies 1990), none have addressed feeding ecology of the MVP during the critical brood-rearing period.

The major objectives of this study were to elucidate factors that influence productivity of MVP Canada geese, and to identify possible limiting resources on the breeding grounds. The approach used was to: (1) document nesting phenology, (2) evaluate the effects of environmental factors and predation on nest success, (3) estimate gosling survival, and (4) describe habitat selection and feeding ecology of MVP Canada geese during nesting and brood-rearing. This information will be useful in estimating annual productivity, and lead to improved fall flight forecasts allowing more precise harvest management.

STUDY AREA

This study was conducted on the south coast of Hudson Bay about 12 km east of Winisk, Ontario (55° 15' N, 85° 00' W). Boundaries of the area were designated arbitrarily to correspond with natural landmarks (generally river channels) and areas of suitable Canada goose nesting habitat (Fig. 1). Thus, the boundaries and size of the study area varied somewhat during the early years of the study as investigators became familiar with which areas were used by geese and which were not. By 1987, the area had expanded from about 5.8 km^2 (the area searched during 1985-86 that was included in later years) to an 11.2 km^2 "core nesting area", and a 1.0 km^2 "peripheral area" that was not searched as intensively as the core; growth of the core area was halted at this point, and these boundaries were used through 1990.

An additional "experimental" study area was established for experimental studies (C. R. Paine, Southern Illinois University, pers. commun.). The experimental area extended east from the eastern border of the core area, and was expanded during 1989-90.

Habitat classification was based on patterns describe by Brokx (1965). Habitat types were widely interspersed and intergraded, making precise classification difficult. The northern part of the core area (from the northern boundary to about 1-1.5 km

A sparse treeline composed of tamarack (Larix laricina) and black spruce (Picea mariana) separated the northern and southern parts of the core area. Tamaracks were also widely scattered throughout much of the study area. The southern core was dominated by a broad expanse of sedge fen, but also included areas of shrub fen, mixed fen, tundra heath, and forest tundra.

The term "study area" is used more generally during the brood-rearing season, but refers primarily to the coastal areas from the area surrounding Tower 1 to the areas surrounding Tower 3 (see Fig. 1). The first vegetative communities inland from the unvegetated tidal flats, were tidal salt marshes dominated by Carex subspathacea and Puccinellia phryganodes. Inland from these marshes were sedge meadows, often with numerous small pools, and mixed fen habitats.

METHODS

Nesting Phenology

The pattern of spring ice breakup on the study area was documented by daily monitoring of stream levels in Strawberry Creek (between the cabin and the study area) and the Flat River (Fig. 1). Nest searches began as soon as spring breakup was underway to facilitate finding as many nests during laying as possible. Early nest searching consisted of 2-5 searchers moving across sections of the study area investigating areas that were not covered with ice, snow, or water (i.e., areas suitable for nesting), especially when tended by a pair of geese. Nest searching became more systematic as more bare ground became available. Late in the nest initiation period, the entire 11.2 km^2 core nesting area was systematically searched by 3-5 searchers walking about 75 m apart in 1988, and 50 m apart in 1989 and 1990. Some additional searching (not systematic) was conducted in the 1 km^2 peripheral area east of the core nesting area.

Initiation was defined as the date the first egg was laid in a nest. Incubation was defined as the period beginning with the date the last egg was laid in a nest, and continued to when $\geq$ 1 egg was known to have been star or hole pipped. More traditional definitions of incubation period and hatch are based on when the young actually leave the eggs (Drent 1975), but when young left the eggs was influenced by web tagging operations in this study. Thus, onset of hatch was a more useful biological measurement in this case.

Methods for marking nests to facilitate relocation varied from year to year. During 1985-87 small plastic stakes (1.5 x 2 cm) bearing the nest identification

number were inserted into the ground alongside the nest, and brightly colored (red, orange and green) flagging tape was tied to a tree or shrub 20-100 m from the nest. During 1988-90, nests were marked with brightly colored flagging tape (about 2.5 x 20-50 cm) typically tied to a shrub or tree 25-50 m from the nest. The compass bearing from the marker to the nest was written on the flag so that the nest could be easily relocated even when the goose was not present. Laying sequences were determined by differential egg staining when possible (Raveling and Lumsden 1977), and eggs were numbered sequentially with a marking pen. The nest identification number was also written on two eggs during 1988-90. Eggs were covered with down and nest material before researchers left nest sites; geese typically cover their eggs when they voluntarily leave their nests for incubation breaks or between layings, a tactic that reduces avian predation (Vacca and Handel 1988).

Nests found during laying were visited daily until laying was complete to determine the onset of incubation. Initiation dates were determined by back-dating from onset of hatch assuming a 27-day incubation period, starting with the date the last egg was laid, and a laying rate of 1.5 eggs/day (Kossack 1950, Cooper 1976). In cases where hatch had progressed past the star-pip or hole-pip stage on the date the nest was visited (at least one damp or fluffy gosling out of the egg), one day was subtracted from that date to yield a date for onset of hatch.

Incubation periods were determined by counting the days between the earliest date the last egg could have been laid in a nest, and onset of hatch. Only nests where the last egg was laid between visits on consecutive days were considered suitable for this analysis. The earliest date the last egg could have been laid in a nest was defined as the last date the nest was visited when the clutch size = total clutch size - 1. It is

likely that some of these eggs were laid the following day, so the average incubation period calculated by this method may be somewhat longer than the actual incubation period.

Nests with known laying chronology were visited two days prior to the predicted hatch date to check for signs of hatch. Nests with unknown laying chronology were visited two days before the earliest predicted hatch date. If no signs of hatch were evident, the nests were revisited every other day until hatch.

Productivity

Spatial Relationships of Nests.--Nest density was determined by locating all nests on the core study area via the systematic searches described under Nesting Phenology, and dividing the number of nests by the area. Densities were determined for the 5.8 km^2 portion of the study area that was searched during all six years, and for the entire 11.2 km^2 core area, which was searched consistently during 1987-90. Nests were mapped on aerial photographs (1:7000) to facilitate relocation of nests, examination of nest distribution, and measurement of inter-nest distance. Bearings were taken from nests to landmarks using Suunto KB-14 and KB-20 compasses. These bearings were used to plot nest locations on the aerial photographs using triangulation from the landmarks.

Inter-nest distances on the entire core area were determined for 1988-90 by measuring the distance between a nest and its nearest neighbor on the photographs. Mean inter-nest distances were compared using analysis of variance and Duncan's Multiple Range Test (PROC GLM, SAS Institute 1990). Spatial relationships of nests

in 1988-90 were examined using nearest neighbor analysis (Clark and Evans 1954, Simmons 1988).

Clutch Size.--Total clutch size (TCS) was defined as the largest number of eggs known to have been laid in a nest. Partial predation of clutches that reached the incubation stage was documented by noting the number of eggs present whenever a nest was visited. Clutch size at hatch (CSH) was defined as the number of eggs remaining in a successful nest at onset of hatch. Goslings leaving nest (GLN) was the number of goslings known or believed to have successfully hatched and left the nest with the parents. Hatch success was the proportion of eggs laid that produced goslings that left the nest. Virtually all nests were visited following departure of the geese to determine if all goslings had left and to check the status of unhatched eggs. The effects of year and nesting phenology on TCS, CSH and GLN were compared using analysis of variance and Duncan's Multiple Range Test (PROC GLM, SAS Institute 1986).

Nest Success.--Nest success was calculated as the proportion of observed nests, including those that were destroyed or abandoned before they were found, in which at least 1 egg hatched. This will be referred to as the Traditional Method throughout this thesis (Klett and Johnson 1982). Because of potential biases and loss of data associated with the Traditional Method (Mayfield 1961, 1975; Miller and Johnson 1978; Bart and Robson 1982; Klett and Johnson 1982), nest success was also calculated using the Mayfield Method. Mayfield estimates of nest success were calculated by raising the daily survival rate to a power equal to the average lifespan (laying + incubation) of successful nests (Klett and Johnson 1982). Nests that were found after they had failed were included in Traditional Method values, but were

excluded from Mayfield Method calculations, because a nest must be under observation for at least one day to be included in the Mayfield calculations.

The proportion of nests surviving to hatch from weekly stages of incubation was calculated for each year based on nests with known chronology. In cases where nest failure occurred over a period of several days between visits, the date of failure was assumed to be halfway between the two visits, similar to the assumption used with the Mayfield Method for calculating nest success. The number of days between the earliest possible date that the last egg was laid (day one of incubation) up to and including the failure date was used to determine the week of incubation during which the nest was lost. Percent survival to hatch was determined from initiation of the nest, and the ends of weeks one, two, and three of incubation.

Nests were classified by fate as successful, depredated/ abandoned, abandoned, collected, nest trap attempt, loss due to flooding/heavy rain, and unknown. A nest was classified as depredated/ abandoned when the entire clutch was destroyed but it was not clear whether the nest had been abandoned prior to destruction. A nest was classified as abandoned if at least one intact egg remained in the nest and it was no longer being incubated. Several nests where the incubating female was collected during 1985-86 as part of a bioenergetics study (Gates 1989) were also excluded from these analyses. A nest was classified as a nest trap attempt if a nest trap was set at the nest. Because of possible biases associated with nest trapping operations (1988-90), all nests where nest trapping was attempted have been excluded from analyses of CSH, GLN and nest success unless otherwise noted.

Visits to nests by investigators have sometimes been associated with reduction in nest success or increases in partial depredation (e.g., MacInnes and Misra 1972).

Because of this possibility, logistic regression was used to evaluate the effect of the number of visits to a nest on its chances of being partially depredated, or failing entirely. Logistic regression is a technique commonly used to investigate the relationship between a binary outcome variable (e.g., success, failure) and one or more explanatory variables (Afifi and Clark 1984, Hosmer and Lemeshow 1989, SAS Institute 1990).

Logistic regression models were developed using the SAS LOGISTIC Procedure and guidelines presented by Hosmer and Lemeshow (1989). The independent variables were the number of visits to a nest, TCS, number of days the nest was under observation, and date the nest was found relative to median initiation date. Number of days under observation was used to add information on the rate of visitation into the model. The date the nest was found relative to median initiation date was used in the model because of the differential probabilities of nests at different stages of incubation surviving to hatch (Mayfield 1975).

The effect of habitat type on nest success was examined by comparing the frequencies of successful and depredated/abandoned nests in different habitat types using G-tests (Sokal and Rohlf 1981). The null hypothesis was that the frequency of successful nests was independent of habitat type. Mean values of height of tallest vegetation and total cover (discussed under nest site selection) were compared between successful and failed nests using t-tests.

Gosling Survival

Goslings were marked beginning in 1986 with size 1 Monel, Ontario Ministry of Natural Resources web tags at hatch, or before hatch at the hole pip stage.

Sometimes it was necessary to enlarge the hole to gain access to the foot, a process which accelerated hatch. In 1988, goslings were also marked with individually coded patagial tags to allow visual identification during brood rearing.

Nesting females were captured on the study area from approximately mid-incubation to hatch using modified falconer's bow traps during 1988-90. Traps were typically sprung the day after they were set. Captured adults were marked with standard leg bands, white on orange alphanumerically coded neck-collars, and radio transmitters. Attempts were made to identify as many previously collared birds nesting on the study area as possible.

Helicopter banding drives were used to recapture marked goslings and parents in late July. In 1988, I attempted to assess the brood size of radio-marked females by periodically homing on radio signals until visual contact was established. Gosling survival was estimated using 2 methods, the Family Method (1986-88 and 1990), and the Marked Adult Method (1988 and 1990). Both methods estimated survival by dividing the number of actual recaptures of web-tagged goslings by the number of expected recaptures. With the Family Method, the expected number of recaptures was derived by summing the original family sizes of all the marked families represented in the banding drive recoveries. With the Marked Adult Method, expected values for gosling recaptures were derived in part from recaptures of marked adults that had successful nests on the core area; the following equations were used:

$$\text{expected recaptures} = \frac{\text{adult recaptures}}{\text{total marked adults}} \times \text{total marked goslings}$$

$$\text{survival} = \frac{\text{actual recaptures}}{\text{expected recaptures.}}$$

Marked adults were assumed to have 100% survival between hatch and the banding drives, and to represent the proportion of the core area population accessible to banding drives.

Estimates of gosling survival using the Marked Adult Method should not be affected by brood mixing, assuming that goslings in mixed and unmixed broods were equally likely to be captured in banding drives. However, estimates could have been affected by total brood loss because marked parents that lose their entire brood through mortality or brood mixing may leave the area, and be unavailable for recapture. If this were the case, the adult recapture rate would be reduced, the number of expected recaptures would be depressed and the estimate of survival inflated.

Radio-marked birds with successful nests were used to provide an index to emigration of adults with successful nests from the area. The proportion of radio marked geese that left the area during brood-rearing was multiplied by the total number of marked birds that had successful nests on the study area. This provided an estimate the number of marked parents that left the area. This number was subtracted from the total number of marked adults. The Marked Adult Method assumed that marked adults that lose their broods and remain in the area have a chance of being captured during banding drives equal to those that retained their goslings.

Radio marked birds were located about twice per week to determine if they were still in the area. More extensive searches for radio marked birds were conducted by helicopter, coincident with banding operations in late July. Flights extended from about 25 km east of the cabin to about 10 km to 32 km (1988 and 1989, respectively) west of the cabin. One pass was made along the coast and a

second pass 5-7 km inland. Detection limits of the telemetry equipment should have extended the range of these searches a minimum of 8 km in all directions. Birds whose signals were not received during these searches were considered to have emigrated from the area.

Life Equation.--Results of productivity investigations were used to develop a life equation for MVP Canada geese as described by Smith (1990).

Habitat Selection and Feeding Ecology

Nest Site Selection.--The pattern of ground emergence on the study area was documented during 1989-90 by walking three 100 m ground emergence transects (GET) on the nesting area daily from 14-28 May, and weekly reconnaissance of the entire study area. Cover of snow/ice, water, wet ground, and dry ground along each GET was estimated by the proportion of steps that fell on snow/ice, water, etc. The 3 GETs were located about 1 km south of the northern border of the study area. GET number 1 was located just east of the Flat River, number 2 about halfway between the Flat and Tamarack rivers, and number 3 just west of the west branch of the Tamarack River (see Fig. 1).

Nests were categorized into 3 site types: mainland (locations $>$ 5 m from water), mainland shore (locations $\leq$5 m from permanent water), and island. These categories were applied when the nest was found, and at hatch during 1989-90, to determine how much site types changed during nesting as water levels on the study area declined. Frequencies of nests in different site types were compared across years using G-tests (Sokal and Rohlf 1981). The null hypothesis was that frequencies of nests found during laying in the three site types were independent of year.

Nests were also separated into four habitat types (mixed fen, shrub fen, sedge fen, and other). Frequencies of nests in the various habitat types were compared across years using a G-test. The null hypothesis was that frequencies of nests in different habitat types were independent of year.

Distance to water and height above water were measured at nests when they were found, and again at hatch or destruction of the clutch. Height of the tallest vegetation within 2 m of the nest was measured as an index of vegetative cover. PROC GLM was used to compare mean height of tallest vegetation between years and between successful and unsuccessful nests. To obtain a more quantitative estimate of vegetative cover, a 1 m-high cover pole was used during 1989-90 (Griffith and Youtie 1988). The pole was divided into ten 10-cm alternating blue and white bands. Cover was measured by placing the pole in a vertical position and observing it 15 m from the nest in the four cardinal directions. Each interval was recorded as being 0%, 50%, or 100% obscured by vegetation. Analysis consisted of summing the values for each interval for each of the directions and dividing the sum by 10 to obtain a value for the amount of coverage for each direction. The sum of the values for the four directions was divided by four to provide a total cover value for each nest. The same type of analysis was performed on the bottom three intervals of the cover pole because cover at this height would presumably be most important for concealing an incubating goose.

Mean total cover values were calculated for different categories of nests (failed, successful, random sites) and t-tests were used to compare the means. The hypotheses being tested were that mean total cover values for different nest categories were equal.

Availability of nest habitat during initiation was examined during 1989-90 in three 1-km^2 sampling plots. The plots were located in three areas with high, moderate, and low nest densities (based on densities during 1985-88). Prior to and during nest initiation, habitat data analogous to data gathered at nest sites were collected at random sites along transects within sampling plots. In 1990, sampling was also conducted along two additional 1-km east-west transects located southeast of the high density plot. Priority was given to plots in the high and moderate density areas in 1990, in order to obtain more habitat information from areas where nest densities were relatively high, to facilitate statistical comparison of nest sites and random sites. For transient variables (height above water, distance to water, and site type), only data from nests found on the sampling plots, and during the period when data were collected at random points, were used for comparison with random sites. Measurements to, and above water were not taken at sites that were flooded or beneath snow or ice, because they were obviously not suitable for nest sites. Measurements of height of tallest vegetation and total cover were also sometimes not possible because of snow or ice conditions. Qualitative information on habitat availability was also obtained by weekly reconnaissance of the entire nesting area.

Mean values of height above water, distance to water, height of the tallest vegetation, and total cover of random sites and nest sites on plots found during the sampling period, were compared with t-tests. Proportions of habitat types at nest sites on the sampling plots, and random sites were compared using G-tests.

Habitat Selection During Brood-rearing.--Habitat use of geese was documented through 2-14 hr tower observation sessions conducted during 1989-90. Because entering towers temporarily displaced geese from the surrounding area, the general

procedure was to enter the tower during the evening (2000-2230) and observe geese the following day. On a few occasions, I entered the tower during early-mid afternoon and, once geese returned to the area (usually 1-3 hours), observed them until dusk that day and until late afternoon (1600-1900) on the following day.

Hourly 360° scan samples of were taken with a spotting scope; the location (habitat type) of all visible geese were recorded during each scan. Geese were separated into four categories: goslings, parents, nonparents (birds that did not nest, or failed in their nesting attempt), and adults of unknown breeding status (unknowns). The proportions of each available habitat type visible from the towers were estimated visually. Data were analyzed on a per tower basis since the number of scan samples taken from each tower, and the habitat availability around each tower were unequal. G-tests were used to determine whether overall habitat use differed from availability (expected values = the proportion of a habitat type $\bar{X}$ total number of geese).

A habitat selectivity index (SI) was calculated for each habitat type, by goose category, for each scan by dividing the proportion of geese feeding in that habitat type by the proportion of that habitat type visible from the tower (Sauer 1983). If a goose category was not represented in a scan (e.g., no goslings in the entire scan), an SI was not calculated for that category for that scan. Mean SI's were calculated for each category and habitat type for each tower. SI's > 1.0 indicated selection for a habitat type (i.e, proportional use exceeded availability), SI's < 1.0 indicated avoidance, and SI's $= 1.0$ indicated proportional use equal to availability. Students t-tests were used to test the null hypothesis that mean SI's $= 0$. Additionally, general information on habitat use was also obtained from biweekly triangulation locations of radio-marked geese.

Feeding Ecology.--General activities (e.g., feeding, loafing) of geese were also recorded during habitat use observation sessions to determine which habitat types were selected for feeding. The impact of geese on the their preferred feeding areas was examined by comparing standing crop and quality of vegetation in areas grazed by geese with standing crop and quality of vegetation in areas that were protected from grazing via exclosures.

Seven 0.9 m-high exclosures were erected in feeding areas between 31 May and 2 June 1989 and on 11 June 1990, before the onset of heavy grazing. Twelve of these were 4 X 4 m and the remaining two were 2 X 2 m and 2 X 4 m. Exclosures were constructed of galvanized chicken wire and 2.5 X 5.1 cm wooden stakes. Exclosures were located in the same general area each year; one was located in exactly the same site both years.

Vegetation samples were collected twice during the brood-rearing period, at 10-day intervals, by removing 0.01 m^2 sections of turf from the exclosures and from grazed areas outside the exclosures (Cargill and Jefferies 1984, Sedinger and Raveling 1986). The samples were collected from areas with uniform cover of vegetation inside and outside the exclosures.

Vegetation on the turf samples was clipped to surface level. All samples were washed over a 2 mm sieve and dead vegetation was removed and discarded. Vegetation samples were dried in a conventional oven at 28-49 °C for 48-60 hours and stored in ziplock bags. Each sample was sorted by species to provide an estimate of the species composition at the exclosure sites. Species were recombined before chemical analysis. The samples were placed in a 50 °C oven for about 48 hours (dried to constant weight) to remove any residual moisture prior to chemical analysis.

Standing crop (g above-ground biomass) was estimated from the dry weight of the samples. Productivity (g dry-weight/m^2/day) was determined from the change in standing crop in exclosures between sampling dates. Nitrogen content, used as the indicator of forage quality (Cargill and Jefferies 1984), was determined using the Kjeldahl method by A&L Analytical Laboratories, Memphis, Tennessee.

Mean standing crop and nitrogen concentrations of vegetation from exclosed and grazed areas were compared with t-tests for each sampling date. Mean standing crop and nitrogen concentration within categories were also compared between sample dates (e.g., all exclosure samples on sample date 1 compared with all exclosure samples on date 2). Following these analyses, samples from areas of high goose use, identified qualitatively through observations in the field and quantitatively by standing crop, were separated and the above analyses were performed separately on areas of high goose use.

Analyses

All '$\pm$' values presented in this thesis represent standard error. Null hypotheses were rejected with $P < 0.05$.

RESULTS

Nesting Phenology

Canada geese began to arrive in the Winisk area 23-30 days ($\underline{x}$ = 26 days) before the onset of nest initiation during the 1985-90 breeding seasons (Table 1). Major arrival usually occurred 4-8 days after the first arrivals were observed. Geese that had been radio marked on the Winisk Study Area in 1988 and 1989 returned considerably later than the earliest arrivals. In 1989, geese were first observed in the area on 19 April, with large numbers arriving by 23 April. Seven radio marked birds returned, one on 6 May, another by 8 May, and the other five birds by 12 May. In 1990, geese were first observed on the study area on 21 April. Two radio-marked birds returned between 3 and 6 May, another between 8 and 14 May, and two more between 14 and 24 May. Geese tended to congregate in bare or semi-bare patches of ground that were available during the period between arrival and major spring breakup.

Spring Breakup and Onset of Initiation.--Extensive flooding occurred on the study area as rapid snow melt coincided with break up of ice on the rivers. Nesting phenology was closely associated with peak spring runoff. Initiation of the earliest nests occurred 1-6 days ($\underline{x}$ = 2.5 $\pm$ 0.8 days, N = 6) prior to the date of peak spring runoff, as measured in Strawberry Creek (Table 1). The median initiation date occurred on 10 May in 1987 and 1988; these have been designated as "early" years for the purposes of analysis. During the other four years of the study (1985, 1986, 1989, 1990), median initiation dates occurred between 16 and 18 May; these have been designated as "late" years.

Timing of onset of nest initiation was relatively stable across years, with 12 days between the earliest and latest dates (2 May 1987, and 14 May 1990), and 8 days between the median initiation dates for those years (10 May, and 18 May). The period when nests were initiated was longer during early years, but most birds initiated their nests over a fairly short period each year, averaging 7 days (Fig. 2). Onset of incubation and onset of hatch followed this same pattern (Figs. 3-4).

Nest initiation dates were determined for the three radio marked birds (CM11, CM12, and CM13) that returned and nested successfully the year after they were marked. CM11 was marked in 1988 and returned to the Winisk area 6-9 days before initiating her nest on 17 May 1989. CM12 was marked in 1989 and returned 16 days before initiating her nest on 22 May 1990. CM13 was also marked in 1989, and returned 3-13 days before initiating her nest on 27 May 1990. All other radio marked birds that returned either did not nest, or failed in their nesting attempts.

The earliest date for onset of incubation on the study area was 7 May in 1987 and the latest was 19 May in 1986 and 1990. Median dates for onset of incubation ranged from 14 May in 1986 to 23 May in 1986 and 1990 (Fig. 3).

The earliest date for onset of hatch on the study area was 3 June in 1987 and the latest was 15 June in 1986 and 1990. Median hatch dates ranged from 10 June in 1987 to 19 June in 1986 and 1990 (Fig. 4).

The relationship between date of peak spring runoff and median dates for onset of incubation and onset of hatch were stable among years. Median date for onset of incubation occurred an average of 8.2 ± 0.3 days (range 7-9 days) after the date of peak spring runoff. Median date of onset of hatch occurred an average of 34.8 ± 0.3 days (range 34-36 days) after the date of peak spring runoff.

Incubation Period.--Incubation period was determined for 38 nests. The distribution of incubation periods was one (3%) of 25 days, 15 (39%) of 26 days, 17 (45%) of 27 days, four (10%) of 28 days, and one (3%) of 29 days; the average incubation period was 26.7 $\pm$ 0.8 days.

Only one suspected dump nest was found during the entire study. There was also only one known overtime nest (incubation past the normal time of hatch; $\geq$43 days in this case) and one possible continuation nest (when a female begins laying eggs in one site but completes the clutch in another) (Cooper 1976).

Productivity

Spatial Relationships of Nests.--Nest density on the Winisk Study Area averaged 6.1 $\pm$ 0.6 nests/km^2 on the 5.6 km^2 area searched 1985-90, and 6.6 nests/km^2 on the 11.2 km^2 area searched 1987-90. Density varied independently of population size as measured by mid-December Goose Surveys and appeared to be related to nesting phenology, with high densities occurring in early nesting years, and low densities occurring in late nesting years (Table 2). Mean inter-nest distances (1988-90 only) were larger ($P < 0.05$) in years with low nest densities (233 and 229 m in 1989 and 1990, respectively) than in years with high nest densities (188 m) in 1988.

Nearest neighbor analysis indicated that the distribution of nests was significantly ($P < 0.01$) clumped during 1988-90. R values were 0.55, 0.54, and 0.55 for 1988, 1989 and 1990, respectively. Qualitatively, the distribution of nests appeared to be very similar during 1986-90. Nests were concentrated in relatively high or hummocky areas such as in the northeast and northcentral portion of the core

area, and along the Tamarack River, much of which is characterized by fairly high channel ridges.

Clutch Size and Goslings Leaving Nest.--Mean TCS across years was 4.75 $\pm$ 0.06 (N = 360). There was significant inter-year variation ($F = 4.67$; 4, 354 df; $P < 0.001$) in mean TCS, but no relationship ($P > 0.26$) between mean TCS and nesting phenology was detected (Table 3). No variation ($P > 0.35$) was detected among years in mean CSH; CSH averaged 4.38 $\pm$ 0.09 (N = 216). Mean GLN did not vary ($P > 0.35$) among years and averaged 3.85 $\pm$ 0.10 (N = 212).

Partial Predation.--Partial predation resulted in losses ranging from 5.3% of eggs laid in 1985 to 9.9% of eggs laid in 1989, and averaged 7.6 $\pm$ 0.8% across years (Table 4). The proportion of nests suffering partial predation did not vary by year ($P > 0.5$; 1985 excluded due to sample size). Herring gulls (Larus argentatus) were believed to be primary agents of partial predation, though numerous other possibilities exist. During 1,474 visits to nests during 1988-90, gulls were seen carrying away eggs on two occasions, and the remains of marked eggs were sometimes found at the bases of gull nests.

No relationship ($P > 0.1$) was detected between the number of visits to nests and partial predation in any single year (1985 and 1990 were excluded due to insufficient data for logistic regression), or with all years combined. Total clutch size combined across years was also not related ($P > 0.28$) to partial predation.

Nest Success.--Nests were considered successful if at $\geq$ one egg hatched and the gosling left the nest. Mean nest success values across years, as calculated by the Traditional and Mayfield methods, were 58.3 $\pm$ 9.9% and 56.1 $\pm$ 9.7%, respectively

(Table 5). For ease and clarity of presentation, nest success values throughout the remainder of this thesis are Mayfield estimates unless otherwise indicated.

Average nest success across years was 62.9 $\pm$ 8.5% with data from 1985 excluded. Nest success varied among years (G = 62.2; 5 df; $P < 0.001$) but did not appear to be associated with nesting phenology. The poor nest success observed in 1985 (22.1%) resulted from unusually heavy rains and subsequent flooding in nesting areas that occurred 9-11 June, well into incubation.

Nest failure appeared to occur at a relatively constant rate throughout the nesting period. Thus, the proportion of nests surviving to hatch increased as the nesting period progressed (Table 6). By the end of the third week of incubation, an average of 93.6 $\pm$ 2.6% of active nests survived to hatch.

The primary cause of nest failure in all years was depredation/ abandonment (Table 7). Eggs were completely gone from most depredated/abandoned nests. Eggshells were virtually intact except for large holes in one side at three nests found depredated in 1990, suggesting depredation by either crows (Corvus brachyrhynchos) or ravens (C. corax) (Reardon 1951). On subsequent visits to these nests, the shells appeared to have been consumed.

No relationship ($P > 0.05$) between the number of visits to a nest and nest failure was detected in any single year (1985 and 1990 excluded due to insufficient data for logistic regression). However, with data from all years combined, logistic regression indicated that the number of visits to a nest was positively associated ($P < 0.001$) with its probability of failure. The resulting model was:

$$\text{logit}(p) = 11.08 + (0.31)(\text{visits}) + (-0.57)(\text{days}) + (-0.42)(\text{date found-median initiation date})$$

and

$$p = e^{logit(p)} / [1 + e^{logit(p)}]$$

where p = the probability of nest failure. TCS was not associated ($P > 0.66$) with a nest's probability of failure and was dropped from the logistic regression model. The number of days under observation, and the date nests were found relative to median initiation date were both negatively associated ($P < 0.0001$) with the probability of nest failure. With all years combined, nests were visited an average of 5.06 times, observed an average of 17.82 days, and were found an average of 9.88 days after the median initiation date. Thus, for an "average" nest, p = 0.27.

Hatch Success.--Excluding data from 1985, hatch success of eggs laid on the study area did not vary ($P > 0.05$) by year, and averaged 58 $\pm$ 4% across years (Table 8). Hatch success of eggs remaining at onset of hatch ranged from 85 to 93% ($\bar{x}$ = 88 $\pm$ 2%; 1985 excluded).

Environmental Influences.--Sample sizes of nests (primarily failed nests) during 1986-90 in the various habitat types were insufficient (expected values <5) in any one year to allow statistical testing of the hypothesis that nest success was independent of habitat type. There were differences ($G = 26.12$; 8 df, $P < 0.001$) in frequencies of use of habitat types between years, so data could not be lumped across all years because of possible biases associated with inter-year variation in nest success (e.g., if geese happened to be concentrated in a particular habitat type in a year with high predator numbers). To avoid these biases, the data were divided into groups: years with relatively high nest success (1986, 1988-89) and years with relatively low nest success (1986, 1990). Data from 1985 were excluded because the flooding that occurred during that year was considered anomalous, and because of

differences in habitat classification. Only the three major habitat types (mixed fen, sedge fen, and shrub fen) were compared because samples sizes of other habitat types, even when lumped, were insufficient for testing (expected values < 5). Ninety-four percent of the nests found during 1986-90 were in one of the three major habitat types. Abandoned nests (6) and those with unknown outcomes (2) were also excluded.

Frequencies of use of different habitat types varied ($G = 21.25$; 4 df; $P < 0.001$) across years with high nest success (Table 9). However, because nest success was similar across these years, little or no bias should result from combining the years. No differences ($P > 0.50$) in frequencies (years combined) of successful and depredated/abandoned nests by habitat type were detected. In years with low nest success, no difference ($P > 0.50$) in frequencies of use of different habitat types was detected (Table 10). There were also no differences ($P > 0.05$) in frequencies of successful and depredated/abandoned nests by habitat type in the combined low nest success years.

No differences were detected in the mean height of tallest vegetation at nest sites between years ($P > 0.37$), or between successful and unsuccessful nests ($P > 0.85$).

No differences in mean total cover values measured with the 1 m-high cover pole were detected between successful (8.6%) and failed (8.9%) nests in 1989 ($P > 0.90$) or 1990 (6.2% and 8.0%, $P > 0.65$). There were also no differences in mean total cover values measured with the bottom 30 cm of the cover pole between successful (25.2%) and failed nests (22.9%) in 1989 ($P > 0.75$) and 1990 (17.5% and 23.2%, $P > 0.30$).

Gosling Survival

Web tags were attached to 840 goslings during the 1986-90 nesting seasons. Banding operations began approximately 33, 45, 44, 36, and 35 days after median hatch date in 1986, 1987, 1988, 1989, and 1990, respectively. Telemetry flights were conducted on 28 July 1988 and 31 July 1989.

Family Method.--One hundred twenty-five goslings were recaptured during 15 banding drives, providing sufficient data to estimate gosling survival for 1986-88, and 1990 (Table 11). In 1989, only one of the 208 goslings web-tagged on the core area was recaptured during the banding drives, preventing calculation of a meaningful gosling survival estimate for that year. The mean gosling survival estimate for the other four years was 64 $\pm$ 5%.

In 6 cases, goslings from the same brood were recaptured in two separate banding drives. In 1988, goslings from three broods (1 of 5, 1 of 8, and 4 of 6) that had marked parents were captured in drives in which their parents were not present. In 1990, two goslings, from an original brood of four of a leg-banded, radio marked (defunct radio) goose, were captured in separate banding drives near the mouth of the Flat River, one on 23 July and the other on 27 July. Goslings that had been banded in the first drive were released immediately, so it is possible that the gosling from this brood captured in the first drive was also present in the second drive. However, the marked parent was not present in either drive. Of the 48 families represented in banding drives of all years (including the lone gosling in 1989), 17 were represented by a single gosling. Mixed marked broods were also encountered in the field on two occasions.

Marked Adult Method.--Nest trapping was attempted at 53 nests on the core area during 1988-90, resulting in the capture and marking of 22 geese (42% success). Fourteen (64%) of these birds had successful nests, for an overall trapping success rate of 26% (trapped birds that hatched at least 1 gosling); one of these birds shed her radio shortly after capture. Six birds (11%) abandoned their nests following capture, and two (4%) other nests were depredated/abandoned following capture. Eleven (21%) birds abandoned their nests, and two more (4%) were depredated/abandoned immediately after the trap was set (i.e., before springing the trap the following day). Five nests (9%) failed at some point between the trapping attempt and hatch. The remaining 13 birds (25%) were not caught because of problems with traps (e.g. not closing properly, or too slowly), or birds sneaking off the nest before we could spring the trap.

Because of small numbers of successful radio-marked geese in any one year, successful radio marked birds from 1988-90 (13) were combined to determine a correction factor for emigration of adults with successful nests from the area. Only one of these birds emigrated, yielding a correction factor of 8%.

All radio-marked birds that did not nest, or whose nests failed, left the area between hatch and telemetry flights during late July banding operations. A telemetry flight was unnecessary in 1990 because all radio-marked birds that had successful nests were still within ground telemetry range.

Goslings from 72 families were web-tagged at hatch in 1988. At least one parent from 19 of these families (26%) was neck-collared and the collar code was identified. Neck-collared parents from three families were recaptured during banding

drives, indicating 50 expected gosling recaptures. Fifty-four goslings were recaptured, yielding a gosling survival estimate of 108%.

Goslings from 32 families were web-tagged in 1990, and at least one parent in 13 of these families (41%) was neck-collared. Four of these birds were recaptured during banding drives, indicating 43 expected gosling returns. Thirty-one goslings were recaptured, yielding a gosling survival estimate of 72%.

Life Equation.--A life equation (Smith 1990) was developed from the results described above for the nesting and prefledging phases of the annual cycle of MVP Canada geese (Table 12). Data from 1985 were excluded because it was considered an aberrant year. The primary reductions in productivity occurred during incubation (total nest loss due to depredation/abandonment) and brood-rearing (gosling mortality).

Habitat Selection and Feeding Ecology

Nest Site Selection.--Virtually the entire study area was covered with snow or ice when we arrived and rivers were frozen. By the time major breakup began on the Flat and Tamarack rivers in both 1989 and 1990 (Table 1), the study area was still about 75-85% covered with snow, water, or ice.

Extensive flooding occurred throughout most of the study area as rivers broke up, due to the sudden flush of meltwater and ice clogging the mouths of the rivers. On 10 May 1990, virtually the entire area between GET 1 and GET 3 was covered with about 40 cm of flowing water. Flood waters decreased gradually over a period of several days with areas in the northern part of the study area along the Tamarack River emerging first, followed by gradual emergence from east to west across the

study area. The northeast section of the study area was the first to become exposed, and this was the part of the core area with the highest nest densities 1987-90.

The pattern of east to west ground emergence was also demonstrated by the 3 GETs. On the last day of nest initiation, the most western GET was still 87% and 85% covered with water in 1989 and 1990, respectively, while the most eastern GET was only 15% and 4% covered with water (Figs. 5-7).

In 1989, nests found during laying were separated into 52% island sites, 35% mainland shore sites, and 13% mainland sites (N = 23). At hatch (or nest failure), these same nests were separated into 9% island, 26% mainland shore, 61% mainland, and 4% mainland/island (a mainland site on a large island).

Significant variation ($\underline{G}$ = 32.75; 6 df; $\underline{P} < 0.05$) in frequencies of site types by year was found for 1988-90 (sample sizes of nests found laying during 1985-87 were insufficient for statistical testing). Few island sites were found in 1988, but this was an early year and water had declined substantially from peak levels before intensive nest searching began. Substantially more island nests were found during 1989 and 1990, and frequencies of site types did not differ ($\underline{G}$ = 0.09; 2 df; $\underline{P} > 0.9$) between these years. There were significant differences ($\underline{G}$ = 26.12; 8 df; $\underline{P} < 0.001$) in frequencies of use of habitat types between years.

Nest Sites Versus Random Sites.--Data were collected at 137 random sites in 1989 and 72 random sites in 1990. Because relatively few random sites were sampled in Plot 3, and few nests were located on there, data from that plot have been excluded from comparisons of random sites and nest sites.

Frequencies of habitat types at random sites and nest sites did not differ ($\underline{P} > 0.1$) in 1989 (Table 12). Frequencies of habitat types at nest sites in 1990 differed

from 1990 random sites ($G = 6.06$; 1 df; $P < 0.025$) and from nest sites in 1989 ($G = 5.93$, 1 df, $P < 0.025$). A higher proportion of nests were in mixed fen sites in 1990. There was no difference ($P > 0.1$) between years (1989-90) in the frequencies of habitat types found at random sites.

Results of random sampling in habitat sampling plots indicated that there was little bare ground available for nesting during initiation (Table 14). Comparison of habitat variables revealed differences between random sites and nest sites only in mean height above water (Table 15).

Habitat Selection During Brood-rearing

Fourteen tower observation sessions were conducted during 1989-90, resulting in 122 scans and 13,441 individual observations of geese. G-tests revealed that no categories of geese selected habitat in proportion to its overall availability (Tables 16-18). SI's indicated that goslings and parents selected tidal marshes and avoided all other habitat types with the exception of the upper marsh around Tower 2, which was used in proportion to its availability (Table 19). Nonparents also selected tidal and upper marshes, and avoided all other habitat types except sedge meadow.

Feeding was the primary activity of all categories of geese (Table 20). Geese were observed feeding during all daylight hours, and as darkness fell at about 2300. Geese generally moved about feeding throughout the day. When high tide approached, geese were often observed moving quickly to meet the water. They often continued to feed while swimming in flooded tidal marshes, but I could not determine whether they were grazing or feeding on material suspended in the tide.

Tower observation sessions indicated a strong preference for tidal marshes but radio-marked birds provided evidence of at least some use of inland areas by brood-rearing geese. Some families were quite sedentary throughout the brood-rearing period, while others were quite mobile (e.g. moving >8 km from the core study area),

Feeding Ecology.--All exclosures were located in tidal marsh areas except for one located in an upper marsh in 1990. Except for traces (<1%) of Hippurus tetraphylla and unknown species, the samples were composed entirely of Carex subspathacea and Puccinellia phryganodes (Dore and McNeill 1980, Porsild and Cody 1980).

No differences ($P > 0.05$) in mean standing crop (g dry weight above ground biomass) or nitrogen concentrations were found between samples from exclosures and grazed areas during the first sampling period in 1989 and 1990 (Table 21). In 1989, only high use areas were sampled during the second sampling period, and standing crop was significantly higher in exclosures than in grazed areas. In the high use areas (Table 22), mean standing crop of vegetation from samples taken within the exclosures was significantly larger than grazed areas during both years. Additionally, mean nitrogen concentration of the second sample in 1990 was higher in grazed areas than in exclosures.

Standing crop in exclosures increased ($t = 2.90$; 8 df; $P < 0.02$) between the first and second samples in 1990 but not in 1989 ($P > 0.05$); no differences were detected in grazed areas ($P > 0.50$) between the first and second samples. In high use areas, standing crop increased in exclosures during both 1989 ($t = 2.89$; 6 df, $P < 0.03$) and 1990 ($t = 3.25$; 4 df; $P < 0.03$), and also in grazed areas in 1990 ($t =$

3.14; 6 df; $\underline{P} < 0.02$). Standing crop increased by 6.1 g/day/m^2 between sampling dates in high use area exclosures in 1989 and 5.3 g/day/m^2 in 1990. In grazed areas, standing crop increased 2.2 g/day/m^2 in 1989 and 2.1 g/day/m^2 in 1990. Thus, grazing resulted in a 64% decrease in net above-ground primary production between sampling dates in 1989, and 60% in 1990.

No differences in mean standing crop or nitrogen concentrations were detected between samples from exclosures in low and high use areas ($\underline{P} > 0.10$). However, species composition did vary between low and high use areas. The proportion of Puccinellia phryganodes ($\underline{x} = 30 \pm 5\%$) was higher ($\underline{t} = 3.85$; 10 df; $\underline{P} < 0.004$) in high use areas than in low use areas ($3 \pm 3\%$) where the vegetation was composed almost entirely (98%) of C. subspathacea.

DISCUSSION

Nesting Phenology

Prenesting Period.--Canada geese consistently arrived on the Winisk study area nearly a month before conditions on the study area were suitable for nesting. This prenesting period (23-30 days) is considerably longer than has been generally been found in other studies of Canada geese.

Raveling (1978) reported that Canada geese (B. c. minima, B.c hutchinsii, and B. c. parvipes), including B. c. interior at Kinoje Lake, 460 km southeast of Winisk, and brant (Branta bernicla) regularly nest 10-13 days after peak arrival at nesting areas or departure from final spring staging areas. He indicated this was the case even in early years when nesting habitat is available upon arrival, although nesting might be delayed in late years until nest sites become available. Raveling also indicated that this was the period of time required for rapid follicle development, which culminates only in ovulation or atresia of follicles, and hypothesized that the stimuli leading to rapid follicle development in Canada geese occur just prior to, or at the time of, migration from final spring staging areas. In contrast, in lesser snow geese (Chen caeurulescens), which commonly nest within 3-5 days of their peak arrival at nesting areas, the stimuli for rapid follicle development occur at the time of migration to final staging areas. Thus, Canada geese should have a more flexible response to conditions at or near the nesting ground than lesser snow geese.

MacInnes and Dunn (1988) supported these hypotheses and reported one extreme example that occurred during an exceptionally late spring at McConnell River, N. W. T. Snow geese initiated laying upon arrival even though 90% of the

ground was still snow covered. The authors noted that one isolated snow-free ridge became littered with eggs, with aggregations of up to 50 eggs. Canada geese arrived at about the same time but delayed nesting for 12 days.

The long prenesting intervals observed at the Winisk Study Area indicate that the stimuli for rapid yolk development in Canada geese nesting along the southern coast of Hudson Bay occur on the nesting grounds, providing even more flexibility to spring conditions than has been observed in other Canada geese. More detailed evidence of this phenomenon was provided by Gates (1989), who found that rapid follicle development did not begin until at least two weeks after peak arrival of geese in the Winisk area in 1985 and 1986.

Canada geese appear to arrive throughout the Hudson Bay Lowlands at roughly the same time each year (Tacha et al. 1991), regardless of conditions on the nesting grounds (Raveling and Lumsden 1977, this study). Conditions at final staging areas may be fairly consistent for most geese that nest in the lowlands, but conditions can vary considerably throughout the lowlands. In some years, nesting areas along the coast of Hudson Bay remain snow or ice covered much later than interior lowlands because of the cold maritime influence the bay. For example, onset of initiation at the Winisk Study Area was up to 25 days later than observed at Kinoje Lake by Raveling and Lumsden (1977), and averaged 6 $\pm$ 2 days later than the latest date for onset of initiation observed by these authors (3 May 1967), which Raveling (1978:298) reported was exceptionally late ("the latest in 17 years"). Clearly, it would not be advantageous for coastal nesting geese to begin rapid follicle development when leaving final staging areas if nesting habitat did not become available for nearly a month.

Onset of Initiation.--The relationship between spring weather (primarily snow melt) and onset of nesting in northern nesting geese has been well documented (Barry 1962, MacInnes 1962, MacInnes et al. 1974, Mickelson 1975, Raveling and Lumsden 1977, Raveling 1978, Abraham 1980, Petersen 1990). Because rapid follicle development in geese nesting at Winisk appears to result from local stimuli, nest initiation by these birds is more precisely linked to when habitat becomes available than has been reported in other studies.

The close relationship between peak spring runoff and nesting phenology provides further evidence that local stimuli are responsible for triggering rapid follicle development. This relationship was observed regardless of whether peak runoff was early (5 May) or late (15 May). The difference in dates between early and late years at Winisk was similar to many of the results reported by Raveling (1978), but no delay in nesting to allow for rapid follicle development was observed in early years at Winisk.

The relatively short period during which nests were initiated, and the compression of this period during late years, exhibited by Canada geese in this study are fairly typical of northern nesting geese (Mickelson 1975, Raveling 1978). By extension, onset of incubation and hatch follow the same basic pattern.

Incubation.--Several workers (Kossack 1950, Brakhage 1965, Mickelson 1975) indicated that incubation begins with the completion of the clutch. However, Cooper (1976) found that rather than beginning incubation abruptly, females became progressively more attentive to the nest as the eggs were laid. Results from time lapse photography at Winisk corroborated Cooper's (1976) findings.

Although incubation begins gradually, before the clutch is completed, the period between when the clutch is completed and onset of hatch is still of interest, primarily for accurate backdating from hatch to determine initiation dates or to predict hatch dates for nests with known laying chronology, and also for comparison with other studies.

Ninety-five percent of the incubation periods measured at Winisk were from 26 to 28 days in length, with 27 days being the most common (45%), followed by 26 (39%), 28-day periods (10%). However, under the definition used in this study, incubation terminated at the onset of hatch, rather than when the gosling actually left the egg. This resulted in about a one day reduction in the measured incubation period. Conversely, because the earliest date the last egg could have been laid in a nest was used as the start of incubation (see methods), the actual incubation periods of some of the nests were probably 1 day shorter than the measured incubation periods.

Incubation periods appear to vary little between northern and southern nesting races. Kossack (1950) and Mickelson (1975) reported average incubation periods of 26 (ranges 25-28, and 24-31) days for giant Canada geese in northern Illinois and cackling Canada geese in Alaska, respectively. MacInnes (1962) indicated that the incubation period for small Canada geese was 24 or 25 days. Several other authors have reported 28-day incubation periods for giant Canada geese (Collias and Jahn 1954, Brakhage 1965).

Cooper (1976:51) measured incubation period at 34 nests and found a 27-day period to be most common (68%) followed by 28 (23%) and 26-day (9%) periods ($\underline{x}$ = 27.1 days, computed from his data), within the same range as incubation periods measured at Winisk, though the distribution was skewed towards longer periods. He

also noted that the variance was probably more a result of inaccuracy of estimating time of laying of the last egg than differential development time, an important point that was not addressed by the other authors above.

Productivity

Spatial Relationships of Nests.--Results of this study indicate that fewer birds nest in coastal areas during years with late spring thaw. Whether this is due to an actual reduction in the number of geese that nest, or to displacement of some geese to inland areas that may become available more quickly, is unknown. Other workers have reported reduced nesting effort in late years (Cooch 1961, Barry 1962, Raveling and Lumsden 1977, Finney and Cooke 1978, Raveling 1978, Petersen 1990), and have often indicated that fewer young birds nest in late years. Nest densities on the Winisk Study Area during 1985-90 were considerably higher ($\underline{x}$ = 6.1 nests/km^2) than at Kinoje Lake during 1967-69 (Raveling and Lumsden 1977:30). These authors reported that nest density was 0.3 nests/km^2 for their study area during 1969, the year with the highest density. It follows that inter-nest distances at Winisk were considerably shorter (188-233 m) than at Kinoje Lake (840-1640 m). As in this study, Raveling and Lumsden (1977) found that inter-nest distance decreased with increasing nest density.

The clumped distribution of nests on the Winisk Study Area was also quite different than observed at Kinoje Lake, where Raveling and Lumsden (1977:29, 46) reported that nests exhibited either a random (study area wide) or significantly overdispersed ("favored fen habitat") distribution. The tendency towards overdispersion has been reported in densely nesting populations of Canada geese

(Klopman, 1958, Vermeer 1970, Ewaschuk and Boag 1972), where the close proximity of nests results in high levels of agonistic territorial behavior throughout the nesting season.

Raveling and Lumsden (1977) noted that, because of the low nest densities and large number ("literally thousands") of visually isolated potential nest sites at Kinoje Lake, it was inconceivable that territorial fighting influenced nest spacing. However, because of the overdispersed distribution of nests, even with changes in density, they concluded that, despite relatively long inter-nest distances, nesting geese were "acutely aware" of their neighbors and spaced themselves equidistantly. Raveling and Lumsden (1977) speculated that overdispersion may function as an anti-predation mechanism (but see Andren 1991).

The clumped distribution of nests at Winisk appears to be the result of different pressures, primarily the pattern of ground emergence during spring thaw. Although nest density on the Winisk Study Area was considerably higher than at Kinoje Lake, mean inter-nest distances were relatively large and densities low compared to areas where high nest density has been implicated as a cause of nest failure (Ewaschuk and Boag 1972). The fact that nest success at Winisk was 80% in 1988, the year with the highest nest density, suggests that territorial behavior has little, if any, influence on nest success at density levels observed during this study.

Clutch Size.--There was significant interyear variation in clutch size at the Winisk Study Area (range 4.42-5.02). However, the variation did not follow the typical pattern of northern nesting geese, which is characterized by small clutch sizes in late years (Cooch 1961, MacInnes et al. 1974, Raveling and Lumsden 1977, Finney and Cooke 1982, Davies and Cooke 1983, Ely and Raveling 1984, MacInnes

and Dunn 1988). The second largest mean clutch size (4.95) occurred in a late year (1989), while the second smallest (4.46) occurred in the earliest year (1987). Thus, spring phenology did not appear to be the major determinant of clutch size near Winisk.

Lack (1954, 1968) proposed that clutch size of waterfowl evolved in relation to availability of food for the female at the time and place of egg laying. Lack's theory was modified by Ryder (1970) for northern nesting geese because they generally arrive on nesting areas when little or no food is available. Several authors have indicated that northern nesting geese are forced to rely on stored reserves acquired during spring migration for both maintenance and egg formation (Barry 1962, Ankney 1977, Ankney and MacInnes 1978, Raveling and Lumsden 1977, Raveling 1978).

Ryder (1970) concluded that the number and size of eggs is limited to provide sufficient material to the young until they are able to feed, and to leave the female with enough reserves to give maximum protection to her eggs. Raveling and Lumsden (1977) and Raveling (1979) supported this conclusion and hypothesized that the proximate cause of cessation of egg laying, and hence clutch size, was the depletion to basal winter levels of some essential material (s), probably protein, stored during spring migration. Raveling and Lumsden (1977:54) found that the last egg is generally the smallest in the clutch and felt that this supported the hypothesis that further egg laying was "precluded by caloric or nutritional incapacity to form an egg when the goose reduces her reserves to the basal winter level." However, in a sample of 120 clutches of western Canada geese, Leblanc (1987) found that the first egg was the lightest in 44% of the clutches, and the last egg was the lightest in 45%.

He also found that captive Canada geese, fed ad libitum, exhibited the same pattern of intraclutch variation as wild geese. Leblanc (1987) suggested that this pattern may be a result of hormonal changes during laying and onset of incubation.

The apparent dependency of egg laying on stored reserves explains the smaller clutch sizes of younger birds, which are lighter in weight and accumulate fewer reserves, and the reduction in average clutch size in years with late spring thaws that have been observed in several studies of northern nesting geese (Cooch 1961, MacInnes et al. 1974, Raveling and Lumsden 1977, Finney and Cooke 1982, Davies and Cooke 1983, Ely and Raveling 1984, MacInnes and Dunn 1988). However, the mechanisms that control the reduction in clutch size in late years have not been documented.

Atresia of follicles has been hypothesized to occur if nest initiation is delayed (e.g. by late spring thaw) beyond completion of rapid follicle development (Raveling 1978); each atretic follicle represents one less egg. However, no studies have clearly demonstrated this (MacInnes and Dunn 1988).

Raveling and Lumsden (1977) noted that small clutches, low attentiveness to nests, and poor hatching have often been attributed to inexperience of the female. They felt that in addition to small clutch sizes, depleted energy reserves may be a major cause for low attentiveness (i.e., geese with depleted reserves leave their nests more often to replenish reserves). By examining the performance of individual geese over a series of years, Hamann and Cooke (1986) found that clutch size increased in lesser snow geese with increasing age. In contrast, MacInnes and Dunn (1988) did not detect an influence of female age on clutch size of small Canada geese at McConnell River, although their data were insufficient to draw definite conclusions.

Aldrich and Raveling (1983) concluded that females improve their foraging ability as they grow older and accumulate greater reserves.

MacInnes and Dunn (1988) examined several factors thought to influence clutch size (additive genetic variance, date of initiation, female age, and fidelity to nest site and mate). All of these variables combined explained only 43% of the variance in clutch size. The authors suggested that the remaining variance probably depended on arrival weight of individual females rather than factors on the nesting grounds.

Prevett et al. (1985) provided evidence of considerable spring feeding by both Canada geese and lesser snow geese along the west coast of James Bay. Gates (1989) and Caithamer (1989) examined the bioenergetics of geese nesting near Winisk during 1985-86, and concluded that food intake during the prenesting interval was much more important to interior Canada geese than previously indicated by Raveling and Lumsden (1977), who observed no feeding prior to incubation. Feeding during the prenesting interval was not examined quantitatively during my study, but geese were frequently observed congregating and feeding on snow-free patches as they became available during the prenesting period. Spring thaw was late near Winisk in both 1985 and 1986, and average clutch sizes were 4.89 and 4.54, respectively. Gates (1989) found that geese relied on food intake to supply most of their energy requirements prior to nest initiation, allowing them to conserve endogenous reserves acquired during spring migration for egg laying and incubation. Thus, the availability of food during the prenesting interval appears to weaken the relationship between clutch size and timing of nesting.

Perhaps some temporal or spatial relationship of food availability induces the decrease in nest density observed during late years. Some geese may be excluded from feeding areas by the dominant behavior of more aggressive birds, as has been observed in Canada geese on the wintering grounds (Raveling 1970), or some other factor. Excluded geese may be forced to rely more heavily on stored reserves for maintenance and may reach the point were nesting is no longer advantageous, while the more dominant geese are able to produce normal clutches. MacInnes et al. (1974) suggested that because geese are long lived birds, lifetime reproductive fitness might be enhanced by skipping a nesting season in return for greater success the following year, if reduced reserves make success in the present season unlikely.

Another possibility is that some geese spend part of the prenesting interval in somewhere other than the actual nesting area, as suggested by the arrival of radio marked birds (although presumably somewhere within the Hudson Bay Lowlands, because of the synchrony of arrival throughout the lowlands). In early years, food may become available to geese wherever they are, while in late years some may remain snow or ice covered while others are open.

Despite the long prenesting intervals discussed earlier, clutch sizes at Winisk were somewhat larger than have been found for interior Canada geese nesting at Kinoje Lake (4.37-4.95) 460 km southwest of Winisk (Raveling and Lumsden 1977), and near Cape Churchill, Manitoba (3.4-4.2 during 1985-90), about 600 km northwest of Winisk (B. A. Allen, Univ. of Wisconsin-Madison, pers. commun.).

Total clutch size is a useful variable for comparing nesting effort between years, regions, and races. However, its value is somewhat limited by potential biases associated with its measurement. Because clutch size varies over time due to

predation (partial and total), abandonment, etc., when nests are found relative to initiation can influence measured total clutch size. Thus, mean CSH and GLN are more useful variables for comparison, but they have not typically been reported in the Canada goose literature.

Clutch size decreased between measurement of TCS and CSH and GLN in every year of this study. The decrease appeared to exert a moderating effect on the interyear variation in clutch size, because no interyear variation in mean CSH and mean GLN was detected. While this may be due to the smaller sample sizes of CSH and GLN, it is interesting to note that the largest decrease (1.18 eggs) between TCS and GLN occurred in 1988, the year with the largest mean TCS.

Partial Predation.--Partial predation exerted a constant but relatively minor influence on the productivity of geese nesting at Winisk compared to total nest failure. In contrast with results presented by MacInnes and Misra (1972), the proportion of nests that were partially depredated did not vary by year ($P > 0.50$), despite varying degrees of research activity, while total nest failure varied dramatically ($P < 0.001$).

MacInnes and Misra (1972) pointed out that estimating natural partial predation is difficult if predators are assisted in finding nests by the activities of researchers (i.e., visitor impact). Predators may be assisted in finding nests by the presence or scent of the researcher, the disturbance that results when nests are visited, or markers left behind to help relocate nests (Picozzi 1975, Strang 1980, Sedinger 1990). However, probably the most important factor relating to partial predation of Canada goose nests is that geese, which would normally defend their nest against predators, especially avian predators, leave their nests vulnerable when displaced by researchers.

No relationship between the number of visits to nests and partial predation was detected during this study. Herring gulls (Larus argentatus) appeared to be the only major avian predator on the Winisk Study Area, although ravens were also observed occasionally and may have been nest predators. At least 3-4 gull nests were present on the study area during 1989 and 1990 and probably in earlier years as well. When we were in the vicinity of their nests, gulls sometimes followed us, but their behavior suggested that they were attempting to drive us away from their nests rather than following us in search of food. Other than during these few occasions, my impression was that we were largely ignored by gulls.

Visits may have resulted in limited partial predation, but I believe such events were incidental, and not necessarily more likely to occur during our visits than during other times when a goose left her nest. Only two observations of gulls taking eggs from nests occurred, and these were under unusual circumstances. The first occurred in 1988 when a goose, whose nest was in the same general area where gull nests were typically found, was accidentally flushed during a systematic search. A gull flew in and took an a egg from the uncovered nest. The second event occurred during 1990 when a goose sneaked off the nest I was approaching when I was more than 300 m away. A gull swooped down almost immediately and flew off with an egg. This was very unusual behavior for geese nesting on the core area, which more typically did not leave their nests until investigators were within 100 m, and often much less than that (e.g. 8-50 m). Because gulls did not generally follow us, they were not typically in the vicinity to take advantage of the brief period between when the goose flushed from her nest and when the investigator arrived, and eggs were always carefully covered at the end of our visits. To the human eye, down covered

nests still appear to be quite conspicuous even though the eggs are covered. However, results of other studies suggest that covered nests are either relatively inconspicuous to avian predators, or they do not associate them with food (Gotmark and Ahlund 1984, Vacca and Handel 1988).

This is similar to results reported by Strang (1980) who concluded that, of avian predators on his study area in Alaska, parasitic and long-tailed jaegers (Stercorarius parasiticus and S. longicaudus), and glaucus gulls (L. hyperboreus), only parasitic jaegers were drawn to people, but that gulls sometimes take eggs from exposed waterfowl nests when people are nearby. Territorial gulls did circle people who approached within 400 m of their nests, and followed them as long as they were in the area. Though initially a defensive reaction, this sometimes resulted in gulls taking advantage of exposed duck or goose nests when the person was not too close to the gull nest (Strang 1980, Sedinger 1990). In contrast, MacInnes et al. (1974) reported that predation resulted in egg losses of 13-31% from 1965-71 at McConnell River, and that about 50% of this was the result of human disturbance. Partial clutch loss was attributed entirely to "human-assisted predation" by MacInnes and Misra (1972; but see also Strang 1980, and MacInnes 1980).

MacInnes and Misra (1972:414) reported that jaegers (Stercorarius spp.), gulls (L. argentatus and L. thayeri), and arctic foxes (Alopex lagopus) were "particularly attracted by human activity and learn to follow biologists in the field." Avian predators have typically been implicated in partial predation that results when geese are displaced from their nests by researchers (MacInnes and Misra 1972, Sedinger 1990). Gotmark and Ahlund (1984:386) reported that great black-backed gulls (L. marinus) were "weakly attracted" to islands where incubating eiders had been flushed,

but detected no differences in clutch size or the frequency of depredated nests between disturbed and control sites). MacInnes (1962, 1980) reported that gulls were attracted to parasitic jaegers feeding at goose nests. Jaegers were not a problem near Winisk. I observed a long-tailed jaeger flying over the study area on only one occasion, in 1989.

Sedinger (1990) detected no effect of visits to black brant nests on predation rates on the Yukon-Kuskokwim Delta, Alaska, and concluded the lack of impact resulted from the attentiveness of brant to their nests, aggression towards avian predators, and to the low abundance of parasitic jaegers in his study area. Indeed, avian predator density was apparently much higher at MacInnes and Misra's (1972) McConnell River study area than at other northern sites where visitor impact has been examined (MacInnes 1962, 1980; Strang 1980).

Vacca and Handel (1988) found that marking the location of artificial goose nests on the Yukon-Kuskokwim Delta with highly visible flags (5 m from the nest) did not significantly increase predation of those nests. Similar to Strang (1980), Vacca and Handel (1988) concluded that investigators attracted predators to the study area, and increased predation of uncovered nests immediately following the visit. However, they also indicated that covering the eggs with down essentially negated the effect of attracting predators during the visit. Gotmark and Ahlund (1984) also stressed the importance of covering nests at the end of a visit.

Nest Success.--Numerous authors have discussed the potential biases associated with calculating nest success and use of the Mayfield Method (Mayfield 1961, 1975, Dow 1978, Miller and Johnson 1978, Hensler and Nichols 1981, Bart and Robson 1982, Klett and Johnson 1982, and others). The close agreement between nest

success values calculated using the Traditional and Mayfield methods suggests that little bias was associated with using the Traditional Method. Such a result would be expected in cases where all nests are found in an area, including those that failed prior to discovery. The agreement between the Traditional and Mayfield methods supports my belief that virtually all active nests were found in this study, as well as many that failed prior to discovery.

Total failure of nests proved to be the major influence, other than nesting effort, on productivity during the nesting season during all years. Unfortunately it was also largely inscrutable. Circumstantial evidence suggests that most of these nests were depredated rather than abandoned and subsequently depredated. Eggs often remained undisturbed for long periods of time at nests that were known to have been abandoned during laying, or during incubation (usually due to nest-trapping activities). This suggests that in years when large numbers of nests were found depredated/ abandoned, at least some nests should have been found with the eggs still intact if many nests were being abandoned. However, with the exception of nests that were flooded in 1985, only 5 such cases occurred during incubation (2 each in 1985 and 1986, and 1 in 1988), except in nests disturbed by research activities (e.g., nest trap or collection attempts).

The inability to distinguish between depredated nests and nests that were abandoned or poorly attended prior to depredation, and what predators were involved, are often major handicaps in trying to understand this phenomenon (Raveling and Lumsden 1977, Anthony et al. 1991). Raveling and Lumsden (1977) attributed cases where there were no egg remains to avian predators because of the locations of most nests (islands) and observations of ravens carrying whole eggs. While herring gulls

certainly carry away goose eggs at Winisk, Canada geese defend their nests against gulls and it seems unlikely that gull predation would result in the loss of an entire clutch, unless the geese were mobbed by gulls or were inattentive to their nest.

Red foxes (Vulpes vulpes) and arctic foxes carry away eggs (Reardon 1951, MacInnes and Misra 1972, Anthony et al. 1991), and both were present in the Winisk area. Arctic fox populations are also known to fluctuate dramatically. Cases of heavy predation by arctic foxes have been noted on both Canada goose and snow goose nests, and arctic foxes have also been associated with almost complete reproductive failure of colonies of black brant on the Yukon-Kuskokwim Delta (Raveling 1989, Anthony et al. 1991). Anthony et al. (1991) noted that arctic fox depredation was not considered serious by earlier investigators on the Yukon-Kuskokwim Delta. They believed that the increase in fox numbers in their coastal nesting area was a result of low tundra vole (Microtus oeconomus) populations in inland habitats, and the presence of walrus carcasses on the coast.

Arctic foxes were the major predators of interior Canada goose nests during a recent study at Cape Churchill, Manitoba (B. W. Allen, Univ. of Wisconsin-Madison, pers. commun.), where observations of foxes increased dramatically between 1989 and 1990. If population dynamics of arctic foxes at Winisk were similar, this may be why nest success declined so drastically between 1989 and 1990. Arctic foxes were sighted on four occasions (core and experimental area) during the nesting season in 1990, including one that was harassing a pair of geese (C. R. Paine, pers. commun.). We also found four dead arctic foxes on the study area in 1990. No observations of foxes occurred during 1988-89 and no carcasses were found.

Logistic regression indicated that research activities affected nest success. However, the relatively low p-value and lack of a significant relationship in any single year suggests that the effects were relatively minor. I also believe that at least some of the nest failure induced by research activities can be regarded as compensatory.

Environmental Factors.--Flooding of nesting areas during incubation resulted in the failure of several nests in 1985. However, this type of flooding was not observed in subsequent years, and long-time residents of the Winisk area indicated that it was an extremely unusual event. Other than in 1985, overall nest success did not appear to be related to weather. Raveling and Lumsden (1977) came to similar conclusions during their study.

Nest success was not influenced by habitat type on the Winisk Study Area, and site types were too transient to be evaluated. The lack of differences in the height of vegetation around nests and in total cover between successful and failed nests suggests that nest success is not influenced by vegetative cover. Similarly, Petersen (1990) found that nest success of cackling Canada geese was not related to structural habitat characteristics. In contrast, Jackson et al. (1988) demonstrated a positive relationship between height of vegetation around lesser snow goose nests and nest success, and Petersen (1990) demonstrated a similar relationship for emperor geese (Chen canagicus). They suggested tall willow bushes protected against predators and harsh environmental conditions.

Gosling Survival.--Estimates of gosling survival are critical to assessment of the productivity of a population. Eberhardt (1987) noted that most estimates of gosling survival rates for geese have been based on one of four methods: (1) comparison of the average number of young hatched per nest with the average size of

broods recorded at some later date (Hanson and Eberhardt 1971, Mickelson 1975), (2) comparison of the total hatch versus the total number of young counted at some later date (Geis 1956, Brakhage 1965), (3) changes in brood size of marked adults (MacInnes et al. 1974, Zicus 1981, Lawrence 1986, Eberhardt 1987), and (4) changes in the size of broods where goslings (Warhurst et al. 1983) or adults and goslings (Lawrence 1986), were marked.

Estimates of gosling survival in this study were derived through the Family Method, basically a modification of Method 2, and the Marked Adult Method. The mean gosling survival estimate via the Family Method (64 $\pm$ 5%; n = 4) was fairly similar to estimates in other studies. However, this method does not address brood mixing or total brood loss. The Marked Adult Method was designed to address these biases, but because of sample sizes of marked birds (1988) and gosling recaptures (1989), it could only be applied in 1990. In 1990, when 41% of the families with successful nests on the core area had a marked parent, the gosling survival estimate (72%) was identical to the estimate calculated by the Family Method. Both methods have their inadequacies, but the close agreement between the two is compelling. The primary problem with the Marked Adult Method was the small sample of radio-marked birds, which were the basis of the estimate of emigration of successful birds from the area.

MacInnes et al. (1974) estimated brood survival of small Canada geese at McConnell River to be 74% from the week before hatch to 35 days post-hatch (unhatched eggs were counted as mortalities) using Method 3 (changes in marked adult brood size). They noted that young rarely changed families and only 3 of 96

marked pairs suffered total brood loss. Mickelson (1975) estimated 87.1% survival for goslings of cackling geese on the Yukon-Kuskokwim Delta using Method 1.

Gosling survival varied from 52 to 78% during 1986-90 in more recent study on the Yukon-Kuskokwim Delta (calculated by Method 3, and adjusted for duration of observation; C. R. Ely, U. S. Fish and Wildl. Serv., pers. commun.), not including total brood loss. Ely also reported total brood loss estimates of 21-41%, but indicated that these results should be interpreted cautiously because of difficulty with determining whether the total brood loss during the first two weeks after hatch resulted from the stress associated with nest trapping (at hatch), or natural events. He also noted that pairs that lost their brood before wing molt often left the area.

Survival estimates derived by methods 1-3 have often been biased by loss of entire broods, brood mixing, or inability to locate all nests and goslings (Zicus 1981, Lawrence 1986). Lawrence (1986) used Method 4 (marked adults and goslings) to address these biases in a study of giant Canada geese in Illinois. By marking both adults and goslings, brood mixing and loss of entire broods were accounted for, assuming that the probability of relocation was equal for all marked birds. Using this method, gosling survival from hatch to fledging averaged 73% during his three-year study.

Lawrence (1986) also used Method 3 (changes in marked adult brood size) to estimate gosling survival. This method accounted for total brood loss but involved the assumption that marked adults and goslings gained and lost goslings at equal rates through mixing. The gosling survival estimate using this method was 70%, similar to the estimate derived using Method 4.

Recapture data, tower observations, and observations in the field from this study suggest extensive brood mixing among geese along the Hudson Bay Coast. Hanson and Smith (1950) and Hanson (1953) assumed that brood mixing was uncommon in MVP geese because low nest densities resulted in few contacts between broods. However, following these studies, the size of the MVP increased from < 200,000 to between 384,000 and 1.1 million during this study, and nest densities and contacts between broods have no doubt increased concurrently (Craven and Rusch 1983, Tacha and Thornburg in press). Clearly, there is ample opportunity for brood mixing along the Hudson Bay coast, where large numbers of geese concentrate in preferred feeding areas.

Brood mixing leads to underestimation of gosling survival in estimates calculated using the family method. Missing members of a brood recaptured at banding are assumed to be dead, but may, in fact, still be alive but no longer in association with their original family. Broods in which no members survive are not available for recapture and do not enter into the calculation of the survival estimate. Thus, total brood loss leads to inflated estimates of gosling survival.

Survival estimates derived from the Family Method were conservative (i.e., they are underestimates of nest success) because of the extensive brood mixing observed during this study, though data are not conclusive. Information provided by the limited number of radio marked geese that had successful nests suggested little emigration, and hence, total brood loss, from the Winisk area. Although some total brood loss occurs, it probably does not offset the negative bias associated with brood mixing.

Habitat Selection and Feeding Ecology

Nest Site Selection.--It appeared that many of the hummocks in nesting areas that were snow free prior to major breakup (e.g., near GET 3) were frozen solidly, and may have been unsuitable for nesting. However, such hummocks may be important cues for rapid follicle development.

The high proportion of nests on island sites encountered during initiation may suggest a preference for island sites over other types. Several authors have reported that northern nesting Canada geese prefer to nest on small islands, or hummocks that appear to be islands at initiation (MacInnes 1962, Mickelson 1975, Raveling and Lumsden 1977, Petersen 1990).

Many nest sites on the Winisk Study Area are small, temporary islands at initiation due to the extensive flooding that occurs during spring breakup. Observations at Winisk during 1989-90 suggest that rather than being preferred sites per se, many of these sites may simply be the first to become available. The island nest sites found during initiation were often small ($<5m^2$) hummocks that became available to geese earlier than surrounding areas that remained inundated. During early nest searching activities, when there was little ground above water, our attention was frequently drawn to the few small islands that had recently emerged. On several occasions, we found previous year's nests on these islands. Few of these sites still appear as islands by the onset of incubation.

Little bare ground was available for nesting during much of initiation, and the mean height above water of nest sites that were above water was significantly greater than at nest sites. Peterson (1990) concluded that height above water was the most influential physical feature for nest site selection by both cackling Canada geese and

emperor geese. She also noted that some potential nest sites on high ground (on pingos) may have been unsuitable because of frozen soil.

The general distribution of nests on the Winisk Study Area appeared to be relatively constant (with the exception of 1985); areas with high numbers of nests in high density years were also the areas with relatively high numbers of nests in low density years. However, inter-year variation in snow and ice cover and melt patterns did result in limited redistribution of nests between years (e.g., different frequencies of nests in different habitat types between 1989 and 1990). Because habitat characteristics do not appear to be related to nest success, variation in habitat availability is probably not important, unless it is influencing the number of birds nesting. The influence of variation in the pattern of spring thaw on the availability and quality of nest sites has been noted in several studies of northern nesting geese (Abraham 1980, Jackson et al. 1988, Petersen 1990).

Habitat Selection During Brood-Rearing.--Canada geese observed during tower observation sessions exhibited an overwhelming preference for tidal salt marshes, and these areas are clearly important for families and nonparents. However, because all towers were in fairly coastal locations, there was little opportunity to observe inland habitats. Data from radio marked geese indicate that some birds do regularly use inland areas. Nonparents were more mobile prior to molt and would often feed in tidal marshes for a while and then fly off to unknown locations. There also appeared to be some back and forth movement between coastal and inland areas by families using the area around Tower 3, which was in a coastal area but was also in close proximity to inland habitats. Because geese in inland areas were not observable, little is known about their habitat use.

Some geese observed during this study, notably CM11, CM12, and CM13, appeared to be attached to a certain area (around Tower 1), but others ranged widely throughout the brood rearing period. Lieff (1973) reported that small Canada geese at McConnell River have strong traditional attachments to certain feeding areas and are reluctant to leave these areas even when they become heavily grazed. The boundaries of the feeding range were not determined by the quality of food, but by the distance from open water, which provided the geese with escape routes from terrestrial predators. Geese near Winisk did not exhibit the reluctance to leave open water that Lieff (1973) observed, perhaps because of habitat differences between the Winisk area and McConnell River.

Feeding Ecology.--Monitoring of vegetation during this study extended only through the middle of July, and hence, does not provide complete documentation of the brood-rearing season. However, this study covered the period when grazing pressure is probably most intense. No differences in standing crop between grazed and ungrazed areas were detected when all exclosures were combined, suggesting that even at currently high population levels, grazing pressure is not extreme. In high use areas, mean standing crop was significantly higher in exclosures during all sampling periods. However, low use areas were not devoid of geese. Two of the low use area exclosures were within view of Tower 1, and geese were often seen feeding near the exclosures. This is also the same general area where three marked birds spent the brood-rearing season.

The reasons for the differential use of these areas are not clear, but may have been related to differences in species composition and physiographic features. Species composition in the low use areas was almost entirely Carex, perhaps because of a

more brackish environment provided by river channels on either side, although it is likely that more seaward sites in the same general area had higher proportions of Puccinellia phryganodes.

The exclosures in high use areas were located near Tower 3 and 3-4 km east of Boulder River. Extensive salt marshes bordered the broad point around Tower 3, and the sedge meadow surrounding the tower was dotted with a large number of pools. Geese often grazed the vegetation (Carex spp.) growing along the margins of these pools. The high use area east of Boulder River was a broad swale sheltered by an extensive beach ridge. This area is also used by snow geese.

Geese consumed about 62% of the net above-ground primary production between the sampling dates in high use areas. Though not directly comparable, Cargill and Jefferies (1984) estimated that geese at La Perouse Bay consumed 80% of the net above-ground primary production throughout the breeding season.

Grazing pressure is probably heaviest during the first two weeks post-hatch, when large numbers of nonparents and families are present. The number of nonparents present in the Winisk area gradually declined as they left the area prior to molt. Vegetation in grazed areas continued to increase in biomass despite the heavy grazing (though not significantly in 1989), suggesting recovery of these areas following the period of most intense grazing.

The only difference in nitrogen levels between grazed and ungrazed areas was detected in the second sample in high use areas in 1990. In general, nitrogen levels appeared to be higher in grazed areas.

High quality food sources are essential to northern nesting geese for growth of goslings, and the replenishment of body protein and fat stores of adults, which are at

their annual lows following incubation (MacInnes et al. 1974, Ankney and MacInnes 1978, Raveling 1979, Sedinger and Raveling 1984). Cargill and Jefferies (1984) indicated the major determinant of forage quality for geese during the brood-rearing season was nitrogen concentration, and noted that adequate nitrogen accumulation is frequently critical for herbivores, because the plants they eat contain a much lower concentration of nitrogen than their tissues.

Geese also require more nutritious and digestible foods than larger herbivores because of their limited ability to digest fiber (Demment and Van Soest 1983 as cited by Bazely and Jefferies 1989). Because plants consumed by geese on the breeding grounds are typically low in nitrogen, which is easily digested, the strategy of geese is to ingest large amounts of forage and digest nitrogen efficiently, at the expense of efficient digestion of many other plant constituents (Owen 1972, Sedinger and Raveling 1984, Buchsbaum et al. 1986, Bazely and Jefferies 1989). Efficient carbohydrate digestion would require slower passage of food, thus decreasing nitrogen intake.

The extensive salt marshes along the coast of Hudson Bay are important sources of high quality forage for geese that nest in this region (Kershaw 1976; Jefferies et al. 1979; Porsild and Cody 1980; Cargill and Jefferies 1984a,b; Bazely and Jefferies 1985, 1986, 1989; Sims et al. 1987, Kerbes et al. 1990). Bazely and Jefferies (1986) noted that post-glacial isostatic uplift results in the appearance of 100 to 200 m of new shoreline every 10 years. Puccinellia phryganodes, a stoloniferous grass, and Carex subspathacea, a rhizomatous sedge, are the primary colonists of the sediments of the tidal flats, and are commonly the dominant plant species in these coastal salt marshes. Both are turf-forming species that grow in areas flooded by high

tides in mid-late summer. Carex subspathacea tends to be more abundant in slightly higher areas (typically inland of Puccinellia phryganodes mats), and in more brackish areas, but their habitats intergrade. "Lawns" of Puccinellia phryganodes and Carex subspathacea are intensively grazed by geese, but they rarely remove entire shoots of these species, and apparently move from area to area, thus avoiding over grazing and allowing the grass to recover (Jefferies et al. 1979, Bazely and Jefferies 1986).

Concern has been expressed that heavy grazing pressure by lesser snow geese and Canada geese may have destructive effects on these important wetland habitats, especially in areas where goose numbers have increased dramatically in recent years (Lieff 1973, MacInnes and Kerbes 1987, Kerbes et al. 1990). Early spring foraging is confined to snow-free areas, and Kerbes et al. (1990) reported that grubbing of roots and rhizomes, and shoot-pulling by lesser snow geese on the west coast of Hudson Bay in the spring, destroys vegetation and results in bare patches of sediment. Because of slow recolonization, erosion and isostatic uplift may preclude the recolonization by the original plant communities. These authors concluded that such destruction may limit further expansion of goose colonies in this region.

In contrast with the destruction caused by spring feeding, intensively grazed marshes of Puccinellia phryganodes and Carex subspathacea require high densities of geese to maintain above-ground production, nitrogen concentration, and species composition (Cargill and Jefferies 1984b, Bazely and Jefferies 1986, Sedinger and Raveling 1986, Kotanen and Jefferies 1987, Kerbes et al. 1990). Grazing increases both the quantity and quality of forage. Cargill and Jefferies (1984b) found that grazed plants of Puccinellia phryganodes and Carex subspathacea had significantly higher total nitrogen than did ungrazed plants, and they maintained high nitrogen

levels until late in the growing season. Net above-ground primary production was also significantly higher in grazed areas. Increased production is apparently dependent upon rapid recycling of nitrogen into sediments through goose feces, although other factors are also involved (Bazely and Jefferies 1985, Hik and Jefferies 1990).

Bazely and Jefferies (1986) found that absence of grazing in salt marsh areas where geese were excluded led to rapid changes in structure and composition of the marsh community. In exclosed areas, Puccinellia phryganodes and Carex subspathacea were replaced by less preferred species that are unable to tolerate heavy grazing and trampling. Thus, they concluded that the existence of the grazed community at La Perouse Bay is strongly dependent on the feeding of the geese.

Cargill and Jefferies (1984b) reported that the total area of Puccinellia phryganodes-Carex subspathacea marsh within La Perouse Bay was 5.4 km^2, and La Perouse was inhabited by about 7000 breeding pairs of snow geese and more than 15,000 goslings (Bazely and Jefferies 1989). Geese are more thinly scattered along the southern coast of Hudson Bay during the breeding season. There were probably between 500-1000 breeding pairs using salt marshes observed during this study, which probably amount to a larger area than the marshes observed at La Perouse Bay. However, geese clearly have some impact on preferred feeding areas.

CONCLUSIONS AND RECOMMENDATIONS

Rapid follicle development in Canada geese nesting near Winisk is triggered by local stimuli; thus, onset of nest initiation by these birds is more precisely linked to when habitat becomes available than has been reported in other studies of northern nesting Canada geese.

Nesting phenology of MVP Canada geese was relatively stable for six years, with median initiation dates varying only about nine days between the earliest and latest years. Nesting phenology was closely associated with the date of peak spring runoff.

Spring phenology was not a primary determinant of annual productivity, but did influence nest density. High densities occurred in years with early springs and low densities in years with late springs. Nest densities in coastal areas near Winisk were much higher than those reported for Canada geese nesting in more inland areas of the Hudson Bay Lowlands.

TCS, CSH, GLN, and nest success were not associated with phenology. While TCS varied slightly between years, CSH and GLN were relatively stable. CSH and GLN are more useful than TCS for comparing nesting effort between years, regions, and races because there are fewer biases associated with their measurement.

Habitats used for nesting varied between years, probably because of the pattern of spring thaw, but were not associated with nest success. Similarly, the vegetative structure around nest sites did not affect nest success.

Partial predation was stable ($\underline{x} = 7.6 \pm 1\%$) among years and was not related to observer influence. Hatch success was also stable among years ($88 \pm 2\%$ of the

eggs remaining at hatch). Nest success varied overall among years, but was stable at 82 $\pm$ 2% from the end of week 2 of incubation through hatch, and 94 $\pm$ 3% from the end of week three.

Family Method gosling survival estimates averaged 64 $\pm$ 5% during the four years this method was used. Both the Marked Adult Method and the Family Method yielded gosling survival estimates of 72% in 1990. These are probably conservative estimates of gosling survival of MVP Canada geese. To my knowledge, they are the only estimates of gosling survival available for B. c. interior.

Major influences on productivity were nesting phenology (via reduced nesting effort in late years), factors that resulted in nest failure (predation/abandonment) during incubation, and gosling mortality.

We now have the ability to estimate production and fall flights of MVP Canada geese prior to when annual regulations are set (Tacha et al. in press) because GLN, nest success (late in incubation), and gosling survival are relatively stable and/or predictable. The stability of most nesting statistics also eliminates the need for extensive groundwork to measure them on an annual basis. Surveys conducted late in incubation would be little affected by inter-year variation in nest success. However, information on nesting chronology will be needed to determine the appropriate dates for conducting aerial surveys. Because of its stable relationship with the nesting phenology, peak runoff could be used as an indicator of nesting chronology, at least for coastal nesting birds. Runoff could be monitored periodically from the air, or by a minimal number of personnel on site. Spring aerial population surveys should be conducted 29 days after peak spring runoff to coincide with the end of the third week of incubation.

Coastal salt marshes are important to MVP Canada geese. Though the MVP is currently very large, grazing pressure in salt marshes is probably less than has been reported in other locations (e.g., La Perouse Bay, McConnell River) where there are high numbers of snow geese. Some marshes do not receive measurable amounts of grazing, even though they are used by geese. Inland areas also appear to be important to some geese. Some geese appear to be attached to certain areas during brood rearing, while others are quite mobile.

Productivity of nesting MVP geese does not appear to be limited by the availability of nesting or brood-rearing habitat at current or proposed population levels. Although the potential exists for the population to undergo substantial increases that could eventually have negative impacts on nesting and brood-rearing areas, the breeding grounds appear to be able to support the 900,000 bird MVP spring population objective, and its associated production, proposed by Tacha and Thornburg (1991).

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Table 1. Arrival and onset of nest initiation by Canada geese relative to peak spring runoff at the Winisk Study Area, Ontario, 1985-90.

Year	Arrival of geese	Onset of initiation	Peak spring runoff
1985	13 April	11 May	12 May
1986	13 April	13 May	15 May
1987	12 April	2 May	5 May
1988	9 April[a]	2 May	8 May[b]
1989	19 April	12 May	14 May
1990	21 April	14 May	15 May

[a]Date is from Peawanuck, about 28 km inland from Winisk. In 1987, geese were also first seen in Peawanuck on 9 May, and arrived in Winisk on 12 May.

[b]Peak runoff occurred on or before this date, which represents the
first day measurements were taken in 1988; water levels were high.

Table 2. Density of Canada goose nests relative to nesting phenology on the 5.8 km^2 portion of the core Winisk Study Area searched consistently 1985-90, and on the entire 11.2 km^2 core area, which was searched 1987-90.

Year	Nesting Phenology	Midwinter[a] population	Nests/km^2	
			5.8 km^2 area	11.2 km^2 area
1985	late	384,000	5.5	--
1986	late	355,000	4.8	--
1987	early	331,000	6.6	6.6
1988	early	611,000	8.8	8.5
1989	late	692,000	5.1	5.3
1990	late	871,000	5.5	5.8

[a]From Mid-December Goose Surveys; these values are from the December of the previous year (Illinois Department of Conservation, unpubl. data).

Table 3. Nesting phenology, total clutch size (TCS), clutch size at hatch (CSH),and goslings leaving nest (GLN) of Mississippi Valley Population Canada geese at the Winisk Study Area, Ontario, 1985-90.

		TCS				CSH				GLN			
Year	Nesting phenology	n	x	SE	DMRT[a]	n	x	SE	DMRT	n	x	SE	DMRT
1985	Late	35	4.89	0.17	ABC	7	4.85	0.63	A	4	4.25	0.85	A
1986	Late	37	4.54	0.18	BCD	28	4.14	0.23	A	27	3.63	0.26	A
1987	Early	67	4.46	0.17	DC	47	4.11	0.20	A	47	3.55	0.22	A
1988	Early	98	5.02	0.11	A	63	4.52	0.17	A	63	3.84	0.19	A
1989	Late	66	4.95	0.11	AB	45	4.56	0.20	A	45	4.16	0.24	A
1990	Late	57	4.42	0.14	D	26	4.39	0.19	A	26	4.08	0.19	A

[a]Duncan's Multiple Range Test, different letters within columns indicate significant ($P < 0.05$) differences between years.

Table 4. Number of Canada goose eggs laid in nests that reached incubation and the number and percentage of eggs lost to partial predation at the Winisk Study Area, Ontario, 1985-90.

Year	No. of eggs laid	No. of eggs lost	% of eggs lost
1985	171	9	5.3
1986	168	11	6.5
1987	299	28	9.4
1988	350	30	8.6
1989	274	27	9.9
1990	193	11	5.7
Total	1455	116	8.0

Table 5. Success of Canada goose nests, calculated by the Traditional and Mayfield methods (Mayfield 1960,1975, Klett and Johnson 1982), among years and relative to nesting phenology at the Winisk Study Area, Ontario, 1985-90.

Year	Nesting phenology	Nest success (%)	
		Traditional Method	Mayfield Method
1985	Late	22.6	22.1
1986	Late	71.8	63.3
1987	Early	47.6	42.8
1988	Early	82.6	80.2
1989	Late	81.8	83.2
1990	Late	43.3	45.1

Table 6. The proportion of Canada goose nests with known laying chronology surviving to hatch from the date of initiation, and the end of weeks 1, 2, and 3 of incubation at the Winisk Study Area, Ontario, 1986-90.

Year	n	% survival from			
		Initiation	End of week 1	End of week 2	End of week 3
1986	10	60	75	75	88
1987	17	47	50	80	100
1988	24	63	81	90	90
1989	26	69	75	82	90
1990	32	44	61	82	100
$\bar{x} \pm$ SE		57 ± 5	68 ± 6	82 ± 2	94 ± 3

Table 7. Fates of Canada goose nests among years at the Winisk Study Area, Ontario, 1985-90.

Fate	1985	1986	1987	1988	1989	1990	Total
n	45	47	103	97	67	74	433
Successful	7[a]	28[b]	49	57	45	26	212
Depredated/ abandoned	10	9	52	8	8	29	116
Abandoned	3	2	2	3	2	5	17
Nest trap attempts[c]	--	--	--	29	11	14	54
Collected[c]	6	7	--	--	--	--	13
Loss due to flooding/rain	11	--	--	--	--	--	11
Unknown	8	1	--	--	1	--	10

[a]Includes two nests that hatched successfully but were collected at hatch (Gates 1989).

[b]Includes four nests that hatched successfully but were collected at hatch (Gates 1989).

[c]Excluded from calculations of clutch size at hatch, goslings leaving nest, and nest success.

Table 8. Hatch success (%) on the Winisk Study Area, Ontario, 1985-90.

Year	No. of eggs laid	No. of eggs at hatch	No. of eggs hatched	Hatch success (%)
1985	170	34	17	10
1986	170	116	98	58
1987	339	193	167	49
1988	367	285	242	66
1989	275	205	187	68
1990	214	114	106	50

Table 9. Distribution and success of Canada goose nests[a] by habitat type in years with high nest success (1986, 1988-89) at the Winisk Study Area, Ontario.

Year	Mixed fen		Shrub fen		Sedge fen	
	Number of nests	Number successful	Number of nests	Number successful	Number of nests	Number successful
1986	9	9	8	7	9	7
1988	49	45	8	7	9	8
1989	20	17	19	17	7	6

[a]Abandoned nests were excluded due to insufficient sample sizes; nests with unknown fates were also excluded.

Table 10. Distribution and success of Canada goose nests[a] by habitat type in years with low nest success (1987 and 1990) at the Winisk Study Area, Ontario.

	Mixed fen		Shrub fen		Sedge fen	
Year	Number of nests	Number successful	Number of nests	Number successful	Number of nests	Number successful
1987	49	32	12	9	6	6
1990	28	15	10	9	3	2

[a]Abandoned nests were excluded due to insufficient sample sizes; nests with unknown fates were also excluded.

Table 11. Gosling survival estimates based on the number of web-tagged goslings recaptured during banding drives divided by the total number of goslings at hatch, in the families represented in banding drives.

Variable	1986	1987	1988	1990
No. of goslings web-tagged	62	148	290	131
No. of families represented at banding	5	9	24	9
No. of banding drives with marked goslings	3	2	5	4
No. of marked goslings	13	27	54	31
Sum of the number of goslings in represented families at hatch	18	46	102	43
Gosling survival (%)	72	59	53	72

Table 12. Life equation during the nesting and brood-rearing phase of the annual cycle of a hypothetical population of 1000 breeding pairs of coastal-nesting Mississippi Valley Population Canada geese (after Smith 1990).

Type of gain or loss	No. of nests	No. of eggs	No. of goslings	Total no. of geese
Initiation	1000	--	--	2000
Abandonment	-20	--	--	2000
Depredation/ abandonment	-18	--	--	2000
Incubation	962	4570	--	2000
Abandonment	-24			
Depredation/ abandonment	-274			
Partial depredation		-347		
Onset of hatch	664	2908	--	2000
Post hatch			2556	4556
Gosling mortality			-920	
Banding			1636	3636

Table 13. Frequencies of habitat types among random sites and nest sites in habitat sampling plots at the Winisk Study Area, Ontario, 1989-90.

Habitat type	1989		1990	
	Random sites	Nest sites	Random sites	Nest sites[a]
Mixed fen	32	5	35	14
Sedge fen	38	4	29	2
Other	10	4	6	1

[a]Frequencies of habitat types at nest sites differed from random sites ($P < 0.025$).

Table 14. Percentages of different ground conditions, and mean height above water (cm) of wet and dry ground sites, at random points within nest habitat sampling plots on the Winisk Study Area, Ontario, 1989-90.

Date	Plot	N	% ground conditions: Under water	Under snow/ice	Wet ground	Dry ground	$\bar{x}$ height above water
1989							
13 May	2	28	82	18	0	0	
14 May	1	35	91	9	0	0	
17 May	2	20	70	5	25	0	4.4 ± 1.6
18 May	1	20	95	0	1	0	10.0
19 May	3	15	73	7	20	0	5.3 ± 2.6
22 May	2	19	32	0	63	5	8.5 ± 1.5
1990							
16 May	2	20	85	5	5	5	11.5 ± 4.5
17-18 May	1	20	80	0	15	5	7.3 ± 2.9
19-20 May	2	20	85	5	10	0	9.0 ± 0.0
21 May	2A	12	83	0	8	8	9.0 ± 1.0

Table 15. Mean values of habitat variables at random sites and nest sites on habitat sampling plots on the Winisk Study Area, Ontario, 1989-90.

	1989						1990					
	Random sites			Nest sites			Random sites			Nest sites		
Variable	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Height above water (cm)	7.5[a]	1.2	19	24.1	4.0	6	8.8[b]	2.8	8	18.4	2.3	8
Distance to water (m)	1.7	0.4	19	2.5	1.7	6	0.5	0.2	10	0.8	0.1	8
Height of tallest vegetation (cm)	48.7	2.1	59	44.1	1.5	10	52.0	2.4	61	79.9	16.6	17
Total cover 1-m pole (%)	7.8	1.5	17	8.1	2.0	10	9.2	2.0	12	6.0	1.6	17
Total cover 30-cm pole (%)	25.3	4.6	17	26.7	6.4	10	29.9	6.5	12	17.2	4.5	17

[a]Means of random sites and nest sites differed (t-test), $P < 0.008$

[b]Means of random sites and nest sites differed (t-test), $P < 0.005$

Table 16. Comparison of habitat availability and habitat use by Canada geese around Tower 1 during brood-rearing at the Winisk Study Area, Ontario, 1989-90.

Habitat available	%	% of observations[a]			
		Goslings (n^b = 2,303)	Parents (n = 1,374)	Nonparents (n = 3,236)	Unknowns (n = 909)
Tidal marsh	72	97	96	76	58
Mixed fen	3	0	1	0	3
Sedge meadow	25	3	3	24	39

[a]Use by all goose categories differed from availability ($P < 0.001$).

[b]n = the number of observations

Table 17. Comparison of habitat availability, and habitat use by Canada geese around Tower 2 during brood-rearing at the Winisk Study Area, Ontario, 1989-90.

Habitat available	%	% of observations[a]			
		Goslings (n^b = 229)	Parents (n = 155)	Nonparents (n = 2,324)	Unknowns (n = 319)
Tidal marsh	5	55	46	49	15
Mixed fen	85	37	51	22	51
Sedge meadow	1	0	0	2	4
Upper marsh	5	8	3	27	30
Mud flats	4	0	0	0	0

[a]Use by all goose categories differed from availability ($P < 0.001$).

[b]n = the number of observations.

Table 18. Comparison of habitat availability, and habitat use by Canada geese around Tower 3 during brood-rearing at the Winisk Study Area, Ontario, 1989-90.

Habitat available	%	% of observations[a]			
		Goslings (n^b = 872)	Parents (n = 580)	Nonparents (n = 893)	Unknowns (n = 247)
Tidal marsh	14	65	66	93	72
Mixed fen	44	11	12	2	21
Sedge meadow	40	24	22	4	7
Mud flats	2	0	0	1	0

[a]Use by all goose categories differed from availability ($P < 0.001$).

[b]n = the number of observations.

Table 19. Mean habitat selectivity index (SI) values for Canada geese during brood-rearing at the Winisk Study Area, Ontario, 1989-90.

Habitat	Goose category	Mean selectivity index[a]		
		Tower 1	Tower 2	Tower 3
Tidal marsh	Goslings[b]	1.3[c]	10.0[d]	5.9[c]
	Parents[e]	1.3[c]	9.0[d]	5.4[c]
	Nonparents[f]	1.1[d]	13.0[c]	6.6[c]
	Unknowns[g]	1.0	4.4[h]	5.8[c]
Mixed fen	Goslings	0.2[c]	0.5[d]	0.1[c]
	Parents	0.2[c]	0.6[d]	0.1[c]
	Nonparents	--	0.2[c]	0.1[c]
	Unknowns	1.7	0.7[d]	0.4[c]
Sedge meadow	Goslings	0.2[c]	--	0.4[d]
	Parents	0.2[c]	--	0.4[d]
	Nonparents	0.6[d]	2.1	0.1c
	Unknowns	0.9	6.6	0.1[c]
Upper marsh	Goslings	--	0.7	--
	Parents	--	0.4	--
	Nonparents	--	3.4[c]	--
	Unknowns	--	2.3	--
Mudflats	Goslings	--	--	--
	Parents	--	--	--
	Nonparents	--	--	0.2[c]
	Unknowns	--	--	--

[a]Mean SIs > 1 indicate selection for a habitat type, mean SIs < 1 indicated selection against a habitat type, and mean SIs = 1 indicate selection proportional to availability of a habitat type (Sauer 1983).

[b]The numbers of scans for which SIs could be calculated for goslings were 56, 18, and 18 for Towers 1, 2, and 3, respectively.

[c]Habitat use differed ($P < 0.0005$) from availability.

[d]Habitat use differed ($P < 0.005$) from availability.

[e]The numbers of scans for which SIs could be calculated for parents were 57, 20, and 18 for Towers 1, 2, and 3, respectively.

[f]The numbers of scans for which SIs could be calculated for nonbreeders were 56, 43, and 18 for Towers 1, 2, and 3, respectively.

[g]The numbers of scans for which SIs could be calculated for unknown birds were 47, 30, and 16 for Towers 1, 2, and 3, respectively.

[h]Habitat use differed from availability ($P < 0.01$).

Table 20. General activities of Canada geese observed from towers during brood rearing at the Winisk Study Area, Ontario, 1989-90.

Activity	% of observations			
	Goslings (n = 3,404)	Parents (n = 2,109)	Nonparents (n = 6,453)	Unknowns (n = 1,475)
Feeding	79	62	80	56
Loafing	11	18	14	37
Locomotion	5	7	4	3
Alert	0	9	0	1
Loaf/alert	0	2	0	1
Other	1	2	1	2
Unknown	4	0	1	0

Table 21. Mean standing crop (dry weight) and nitrogen concentration of vegetation samples collected from exclosed and grazed areas on the Winisk Study Area, Ontario, 1989-90.

Date	Sample type	n	$\bar{x}$ standing crop (g/m^2)	$\bar{x}$ % nitrogen
1989				
10-11 July	Exclosed	7	100.0 ± 13.7	2.33 ± 0.13
	Grazed	7	83.9 ± 16.4	2.32 ± 0.06
20 July	Exclosed	4	143.4 ± 19.2[a]	1.78 ± 0.18
	Grazed	4	78.4 ± 11.2	2.03 ± 0.19
1990				
6 July	Exclosed	6	82.2 ± 11.9	2.40 ± 0.15
	Grazed	7	70.1 ± 13.6	2.52 ± 0.12
16 July	Exclosed	4	135.0 ± 13.5	2.15 ± 0.22
	Grazed	5	85.0 ± 22.2	2.48 ± 0.10

[a]Means of exclosed and grazed areas were significantly different ($P < 0.03$); all samples were from high use areas.

Table 22. Mean standing crop (dry weight) and nitrogen concentration of vegetation samples collected from exclosed and grazed in high use areas on the Winisk Study Area, Ontario, 1989-90.

Date	Sample type	n	$\bar{x}$ standing crop (g/m^2)	$\bar{x}$ % nitrogen
1989				
10-11 July	Exclosed	4	82.4 ± 9.0[a]	2.44 ± 0.22
	Grazed	4	56.6 ± 3.2	2.41 ± 0.08
20 July	Exclosed	4	143.4 ± 19.2[a]	1.78 ± 0.18
	Grazed	4	78.4 ± 11.2	2.03 ± 0.19
1990				
6 July	Exclosed	3	71.8 ± 11.1[a]	2.31 ± 0.22
	Grazed	4	42.9 ± 1.4	2.54 ± 0.09
16 July	Exclosed	3	124.4 ± 11.8[b]	2.05 ± 0.06
	Grazed	4	63.5 ± 6.6	2.53 ± 0.11[c]

[a]Means of exclosed and unexclosed areas were significantly different ($P < 0.03$).

[b]Means of exclosed and unexclosed areas were significantly different ($P < 0.005$).

[c]Means of exclosed and unexclosed areas were significantly different ($P < 0.02$).

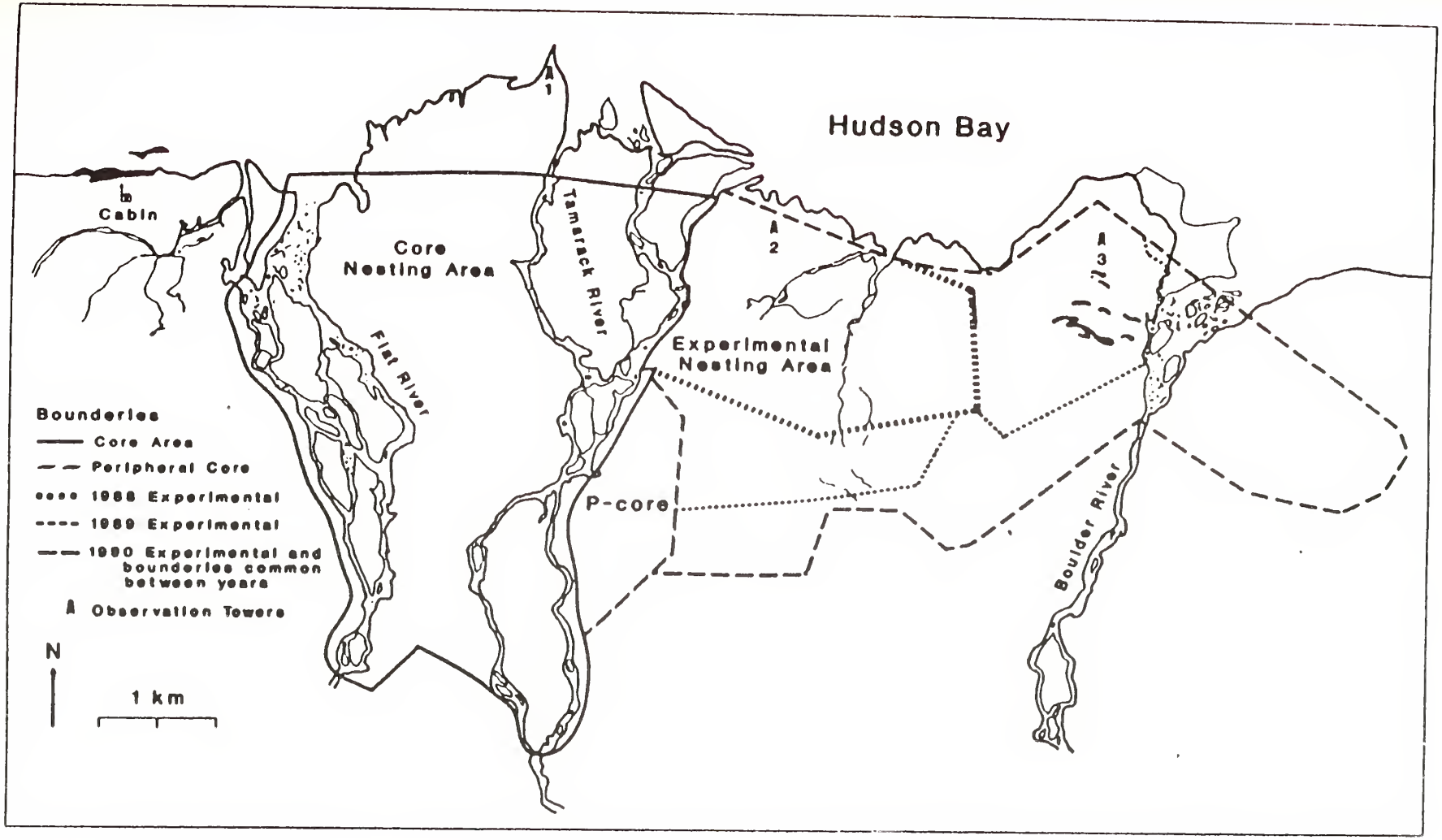


Figure 1. The Winisk Study Area, located 12 km east of Winisk, Ontario (Map courtesy of C. R. Paine).

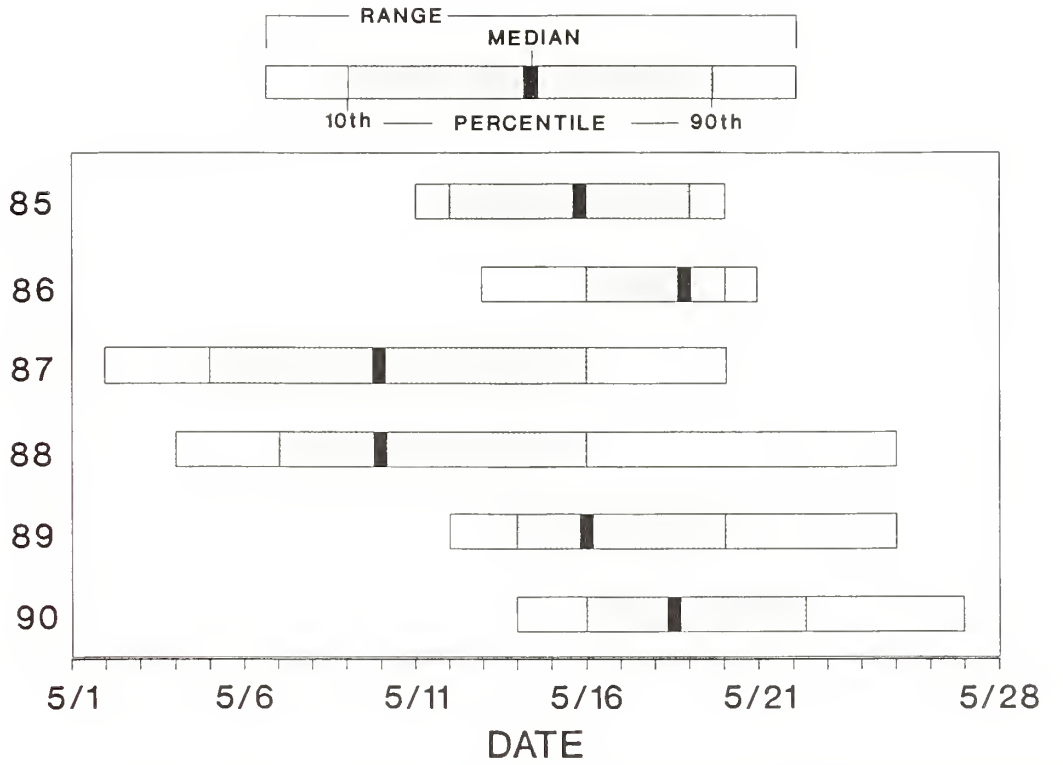


Figure 2. Phenology of onset of nest initiation by Canada geese at the Winisk Study Area, Ontario, 1985-90.

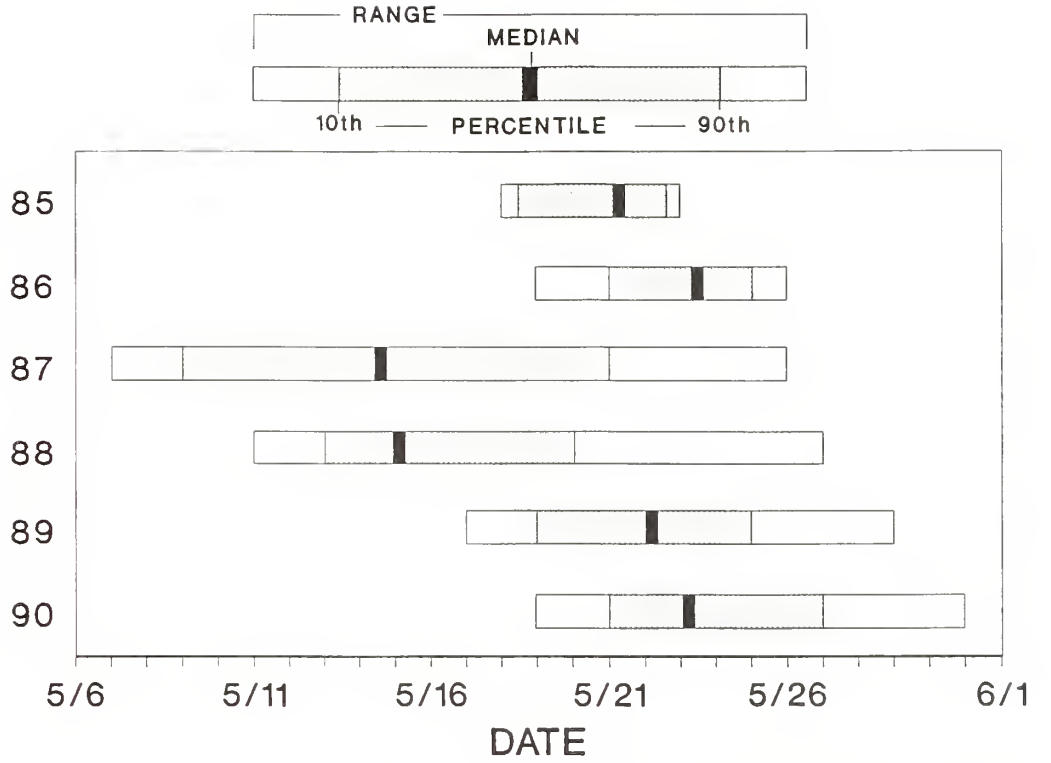


Figure 3. Phenology of onset of incubation by Canada geese at the Winisk Study Area, Ontario, 1985-90.

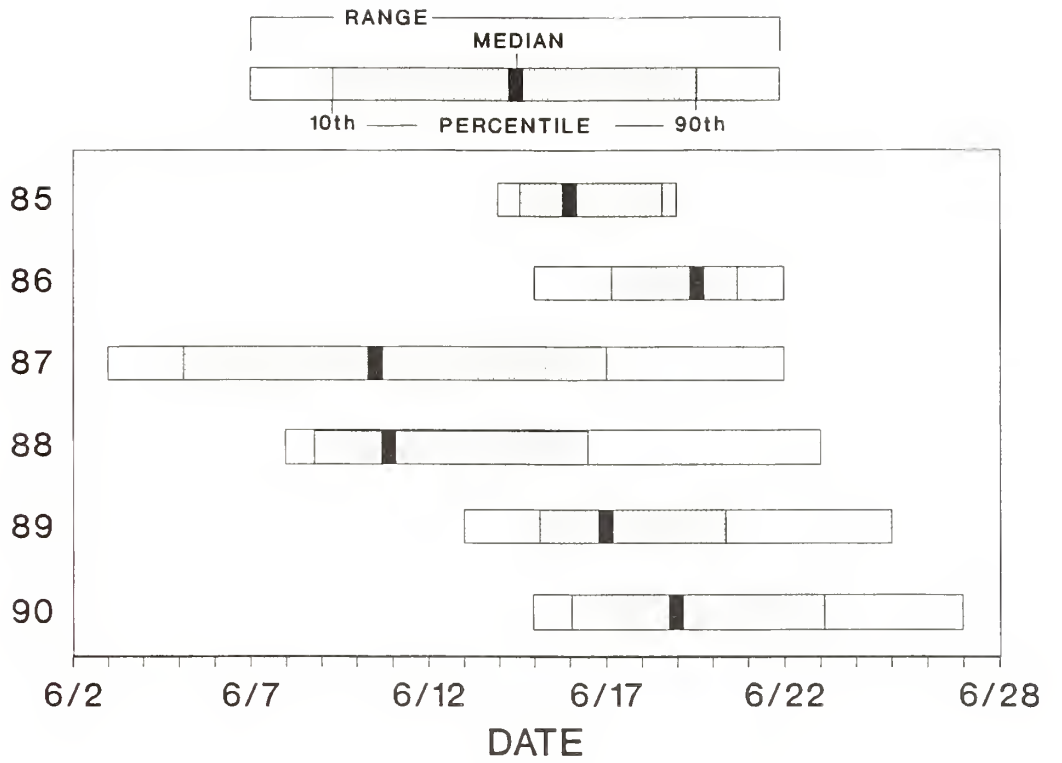
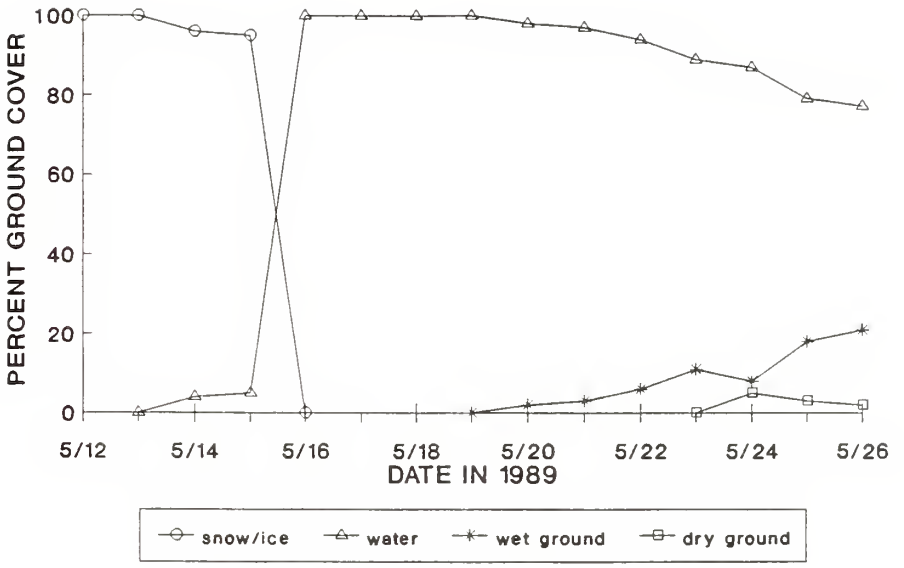


Figure 4. Phenology of onset of hatch of Canada goose nests at the Winisk Study Area, Ontario, 1985-90.



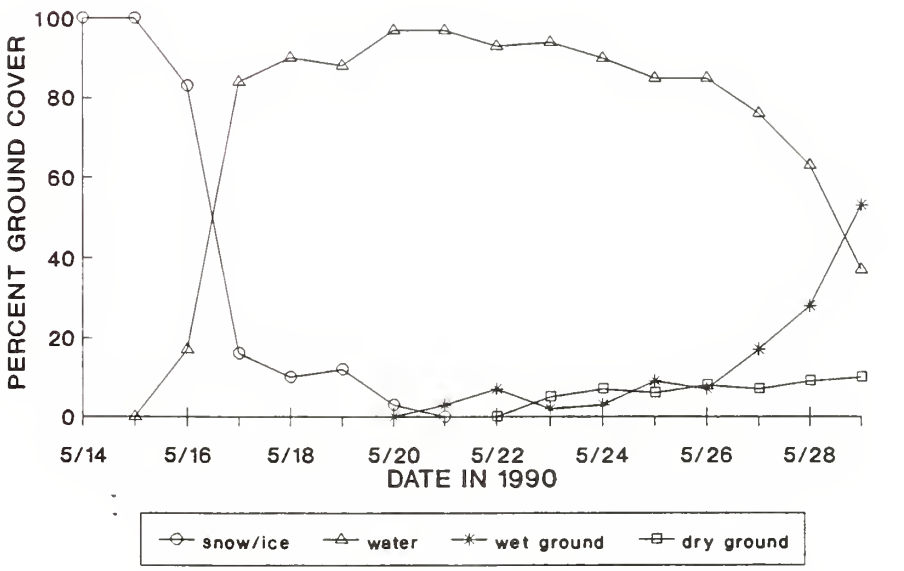
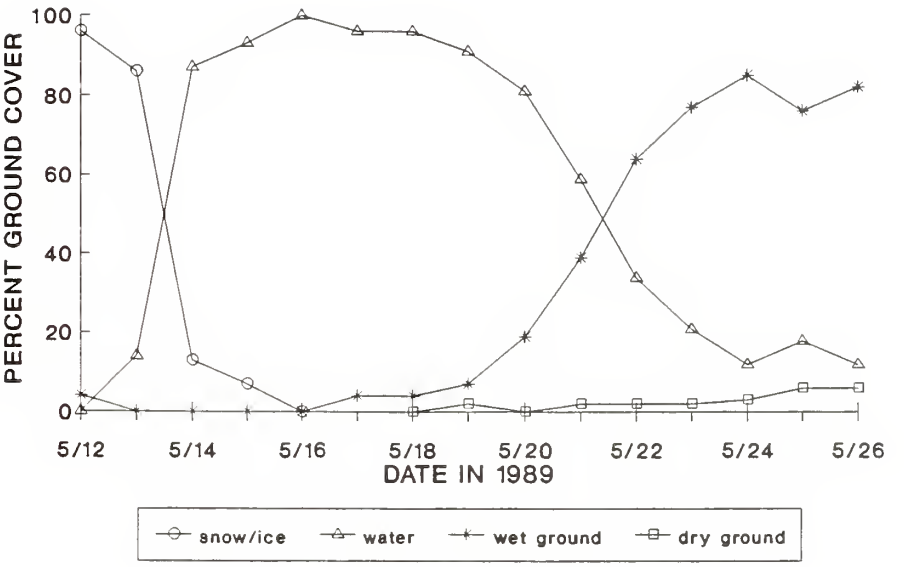


Figure 5. The pattern of ground emergence at ground emergence transect number 1, near the Flat River, 1989-90



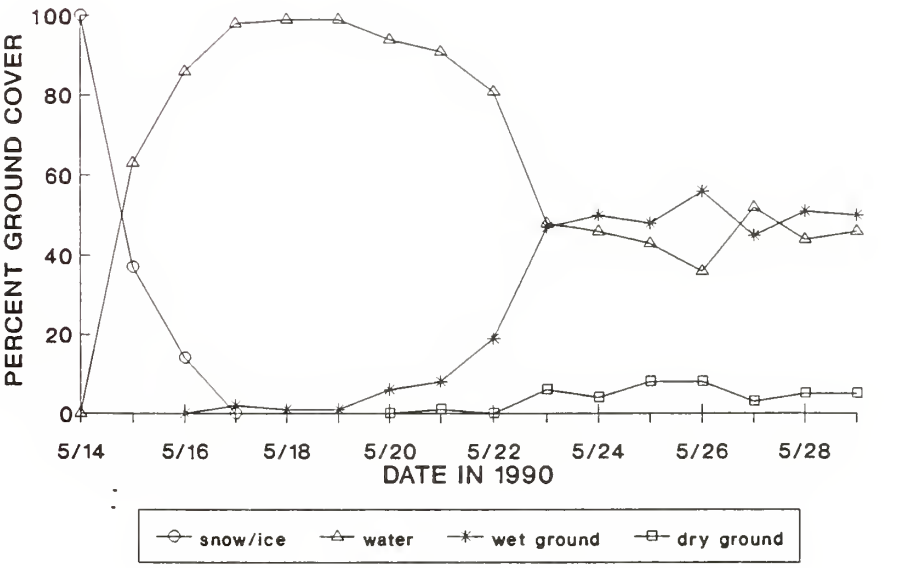
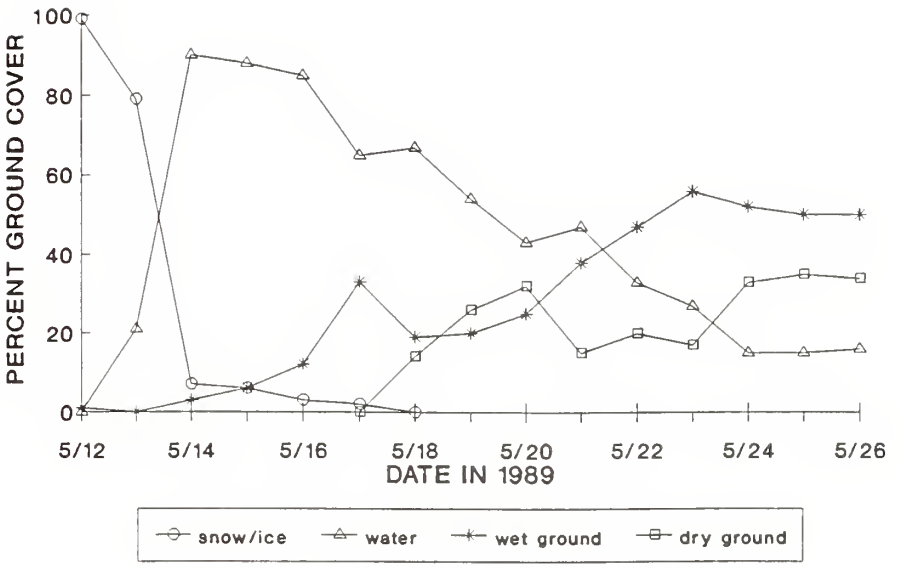


Figure 6. The pattern of ground emergence at ground emergence transect number 2, about halfway between the Flat and Tamarack rivers, 1989-90.



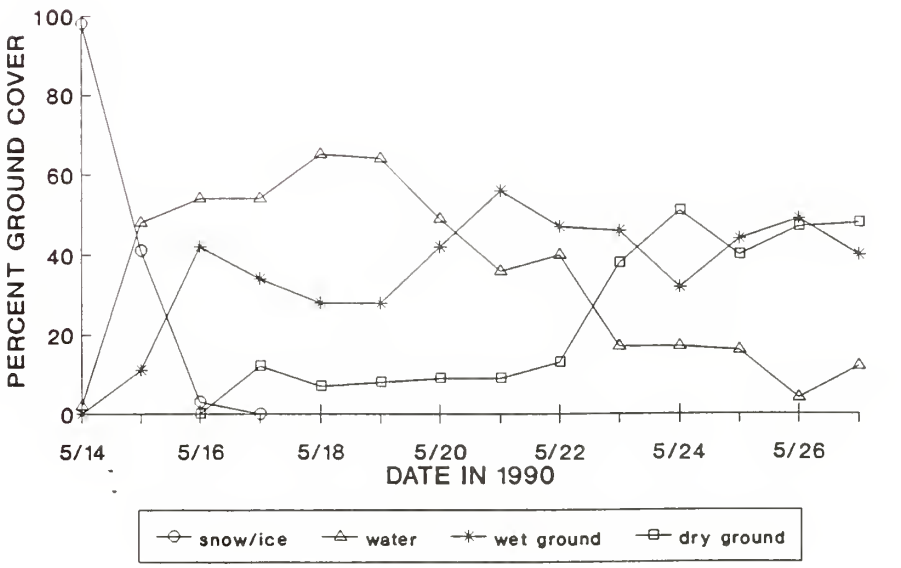


Figure 7. The pattern of ground emergence at ground emergence transect number 3, near the Tamarack River, 1989-90.